

## A revision of the *Thyropygus allevatus* group. Part 1: the *T. opinatus* subgroup (Diplopoda: Spirostreptida: Harpagophoridae)

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## Abstract

The *Thyropygus opinatus* subgroup of the *T. allevatus* group is revised. The *T. opinatus* subgroup corresponds to the genus *Cornugonus* Demange, 1961, which is formally synonymized under *Thyropygus*. Eight new species are described from Thailand: *T. bearti* **n. sp.**, *T. brachyacanthus* **n. sp.**, *T. loxia* **n. sp.**, from Suratthani province, *T. bispinus* **n. sp.**, from Uthaithani and Phrae provinces, *T. bispinispatula* **n. sp.**, from Chumphon province, *T. chelatus* **n. sp.**, from Nakhonsrithammarat province, *T. cristagalli* **n. sp.**, from Phang Nga province and *T. erectus* **n. sp.**, from Satun province. The other species of the *T. opinatus* subgroup, viz., *T. opinatus* (Karsch, 1881), **n. comb.**, *T. floweri* (Demange, 1961), **n. comb.**, *T. implicatus* (Demange, 1961), **n. comb.**, and *T. inflexus* (Demange, 1989), **n. comb.**, are redescribed. New records are given for *T. opinatus*, *T. implicatus* and *T. floweri*. The type locality of *T. floweri* is shown to be in Thailand rather than Malaysia.

**Key words:** millipede, taxonomy, new species, Thailand

## Introduction

The family Harpagophoridae is “probably the most characteristic and conspicuous element in the milliped fauna of the Oriental Region” (Hoffman, 1975). Although species of the polydesmidan family Paradoxosomatidae are far more diverse and numerous, harpagophorids are certainly very prominent members of the Oriental fauna, reaching up to 25 cm in length. However, the taxonomic treatment of this family by previous authors has been problematic.

The genus *Thyropygus* Pocock, 1894, is the largest genus of Harpagophoridae in Southeast Asia. It has had a complicated history but, mainly due to the work of Hoffman (1975), the genus is now quite well circumscribed. Hoffman (1975) explained why *Thyropisthus* Attems, 1942, is a synonym of *Thyropygus* and provided a very useful account of the genus. We adhere to Hoffman’s concept of *Thyropygus* and even widen it slightly by formalizing the synonymy of *Cornugonus* Demange, 1961, tentatively suggested by Hoffman (1975, 1982) and Demange (1989).

*Thyropygus* (incl. *Cornugonus*) currently includes 35 named species and a number of named subspecies (Jeekel, 2006). The genus is broadly distributed in SE Asia: Thailand, Myanmar, Vietnam, Laos, Cambodia, continental Malaysia, Sumatra, Java, and Borneo (Jeekel, 2006; Enghoff, 2005).

## Materials and methods

Newly collected specimens were hand-collected and preserved partly in 70% ethanol, partly in a freezer at -20 °C for subsequent molecular studies. Specimens were examined from the following collections:

- Museum of Zoology, Chulalongkorn University, Bangkok, Thailand (CUMZ)
- Muséum national d’Histoire Naturelle, Paris, France (MNHN)
- The Natural History Museum Basel, Switzerland (NHMB)
- Senckenberg-Museum, Frankfurt a.M., Germany (SMF)
- Natural History Museum of Denmark (Zoological Museum), University of Copenhagen, Denmark (ZMUC)
- Zoologische Staatssammlung, Munich, Germany (ZSM)

Drawings were made using a stereo microscope. Photographic illustrations were made with a Leica DC300 digital camera mounted on a Leica MZ16A stereomicroscope. Auto-Montage Pro software from Syncroscopy was used for image-stacking and 3D focus expansion. Scanning electron micrographs (SEM) were obtained with a JEOL JSM-6335F.

We have focused very much on adult males although adult females and a few juveniles were also available

for study. Although there have been some attempts to use female characters in harpagophorid taxonomy (e.g., Demange, 1961), at the present stage it is the males, and in particular the male gonopods, that provide the vast majority of informative taxonomic characters in this family, as in so many other millipede groups.

### Genus *Thyropygus* Pocock, 1894

*Thyropygus* Pocock, 1894: 380

*Thyropisthus* Attems, 1942: 86, synonymized by Hoffman (1975)

*Cornugonus* Demange, 1961: 177, **new synonym**

See Hoffman (1975) and Jeekel (2006) for extensive synonymies.

**Diagnosis.** No proper, up-to-date diagnosis of *Thyropygus* is available. The genus was placed in the subfamily Harpagophorinae by Demange (1961) and in the tribe Thyropygini by Hoffman (1975). The circumscription of Thyropygini was later modified by Jeekel (2006). The following diagnosis of *Thyropygus* has been extracted from these authors:

- ozopores starting on body ring 6
- body rings not strongly wrinkled dorsally
- stigmatic grooves very long, reaching at least the middle of the leg prefemora
- postfemur and tibia of male walking legs with ventral soft pads
- gonopod sternum present, triangular
- gonopod telopodite with a femoral and mostly also a tibial spine, but without numerous spines along all its length
- prostatic groove terminating apically on a solenomere or prostatic lobe (apical palette of telopodite) in a narrowly expanded area set with a series of long, slender, stiffened, usually pigmented spines (“blepharochaetae” of Hoffman, 1975)
- apical palette voluminous, more or less expanded, forming a somewhat gutter-like structure

Further revisionary work on harpagophorids is likely to lead to modification of this diagnosis.

Hoffman (1975) grouped the species of *Thyropygus* into four species groups: the *allevatus*, *aterrimus*, *luxuriosus*, and *erythropleurus* groups. The last group contains the type species of *Thyropygus*, *T. erythropleurus* Pocock, 1894 (Sumatra) and might alternatively be termed “*Thyropygus* s.s.”

The present paper is the first in a planned series focused on the *T. allevatus* group.

### The *Thyropygus allevatus* group

As defined by Hoffman (1975), this group contains *Thyropygus* species in which both tibial and femoral spines are present on the gonopods, the tibial spine being very long and recurved proximad towards the femoral one.

Hoffman (1975) referred 11 taxa to this group and suggested that two further species, described in *Cornugonus*, might also belong to this group. Considering new species and taxonomic changes since 1975, the following species currently belong to the *T. allevatus* group (names given here are as in Jeekel 2006, except that *carli* is given full species status, cf. Enghoff, 2005):

*Thyropygus allevatus* (Karsch, 1881)

*Thyropygus carli* Attems, 1938

*Thyropygus confusus* Attems, 1938

*Thyropygus cuisinieri* Carl, 1917

*Thyropygus globulus* (Demange, 1989)  
*Thyropygus hoffmani* (Demange, 1961)  
*Thyropygus ligulus* (Demange, 1961)  
*Cornugonus bifurcus* (Demange, 1986)  
*Cornugonus enghoffi* (Demange, 1989)  
*Cornugonus floweri* Demange, 1961  
*Cornugonus implicatus* Demange, 1961  
*Cornugonus inflexus* Demange, 1989  
*Cornugonus opinatus* (Karsch, 1881)

*Thyropygus allevatus* (Karsch, 1881), the ‘type species’ of the *T. allevatus* group, is a common species recorded from all over Thailand and also from Vietnam, Laos, Cambodia and continental Malaysia (Enghoff, 2005). However, it still presents many taxonomic problems. There are many synonyms of *T. allevatus* (see Enghoff 2005), and several subspecies have been recognized, but the considerable variation in both somatic characters and gonopods still needs a comprehensive analysis.

### The status of *Cornugonus* Demange, 1961

According to Demange (1961), the main differences between *Thyropygus* (= *Thyropisthus*) and *Cornugonus* are the presence, in *Cornugonus*, of a spatulate lobe at the apical part of the telopodite, and an additional mesal projection of the gonopod coxa.

Hoffman (1975) mentioned that two species which Demange had described in the genus *Cornugonus* probably belong to the *T. allevatus* group, referring to figs. 248 and 252 in Demange (1961). Having examined specimens of both species in question (*C. opinatus* and *C. implicatus*), we agree that the telopodites illustrated there are indeed very similar to those of *allevatus*. There is the difference that these two species have a separate spatulate lobe on the telopodite, but this probably does not warrant separation at the generic level. The same applies to *C. floweri* and *C. inflexus*, of which we have also examined specimens.

Demange (1986, 1989) described two new species of *Thyropygus* (actually in *Thyropisthus* because he did not accept Hoffman’s synonymisation), *T. bifurcus* and *T. enghoffi*. Both species agree with ‘*Cornugonus*’ in having an internal additional projection on the gonopod coxite. They don’t, however, have the additional spatulate lobe on the telopodite. Furthermore, they agree in that the femoral spine is double in both, whereas it is simple in ‘*Cornugonus*’ (but see *Thyropygus cristagalli* n. sp.).

On the other hand, the spatulate lobe at the apical part of the telopodite is also found outside *Cornugonus*, viz., in *Thyropygus peninsularis* Hoffman, 1982. This species (holotype examined, NHMB) has a very short additional mesal projection of the gonopod coxa. Nevertheless, it does not belong to *T. allevatus* group because the tibial spine is not recurved proximad toward the femoral spine.

Most recently Jeekel (2006), in his bibliographic catalogue of Asian Harpagophoridae, maintained *Cornugonus* as a valid genus and adopted a broader concept of it, including *T. bifurcus* and *T. enghoffi*, as well as *Thyropygus anurus* Pocock, 1896 from Myanmar. According to figs. 39–43 in Demange (1960), the last species has a lateral lamellar lobe at the apical part of telopodite and a very small mesal process of the anterior coxal fold, suggesting a relationship with other ‘*Cornugonus*’ species in the *T. allevatus* group. However, *T. anurus* does not belong to the *T. allevatus* group as defined here because the character of the tibial spine is not concordant with the condition of this character in the group.

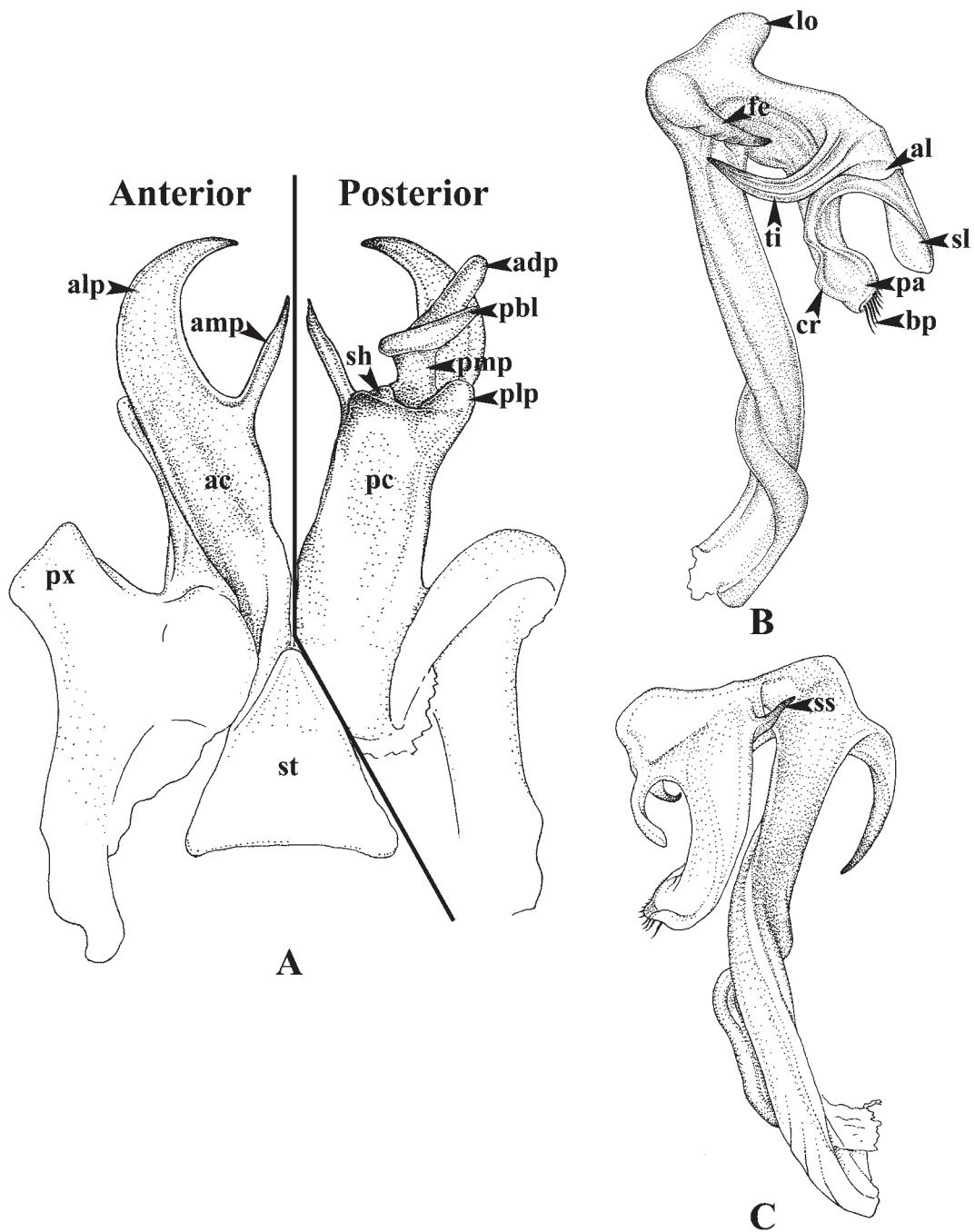
On this basis, we propose not to maintain *Cornugonus* as a separate genus but to synonymize it under *Thyropygus*. More specifically, at least the Thai species so far classified in *Cornugonus* belong to the *T. allevatus* group.

## General description of gonopod structure in the *Thyropygus allevatus* group

The gonopods of harpagophorids consist of 1) an unpaired sternum (usually triangular, sometimes missing), 2) a pair of enlarged coxal parts each forming an elaborate tube, and 3) a pair of telopodites each consisting of a slender basal part which is concealed within the coxal 'tube' and a free distal part with a number of spines, lamellae and other differentiations, notably a row of spines distally. Previous authors have tried to homologize the different parts of the telopodite with normal podomeres: prefemur, femur, postfemur, tibia, and tarsus. We do not subscribe to this approach but nevertheless, for practical reasons, retain a few terms deriving from it, viz., femoral spine and tibial spine.

In papers by previous authors several different terminologies for gonopod structure were used. For this reason we give here our definition of terminology for the structure of the *T. allevatus* group gonopod (Figs. 1, 2) to clarify identification and classification, as follows:

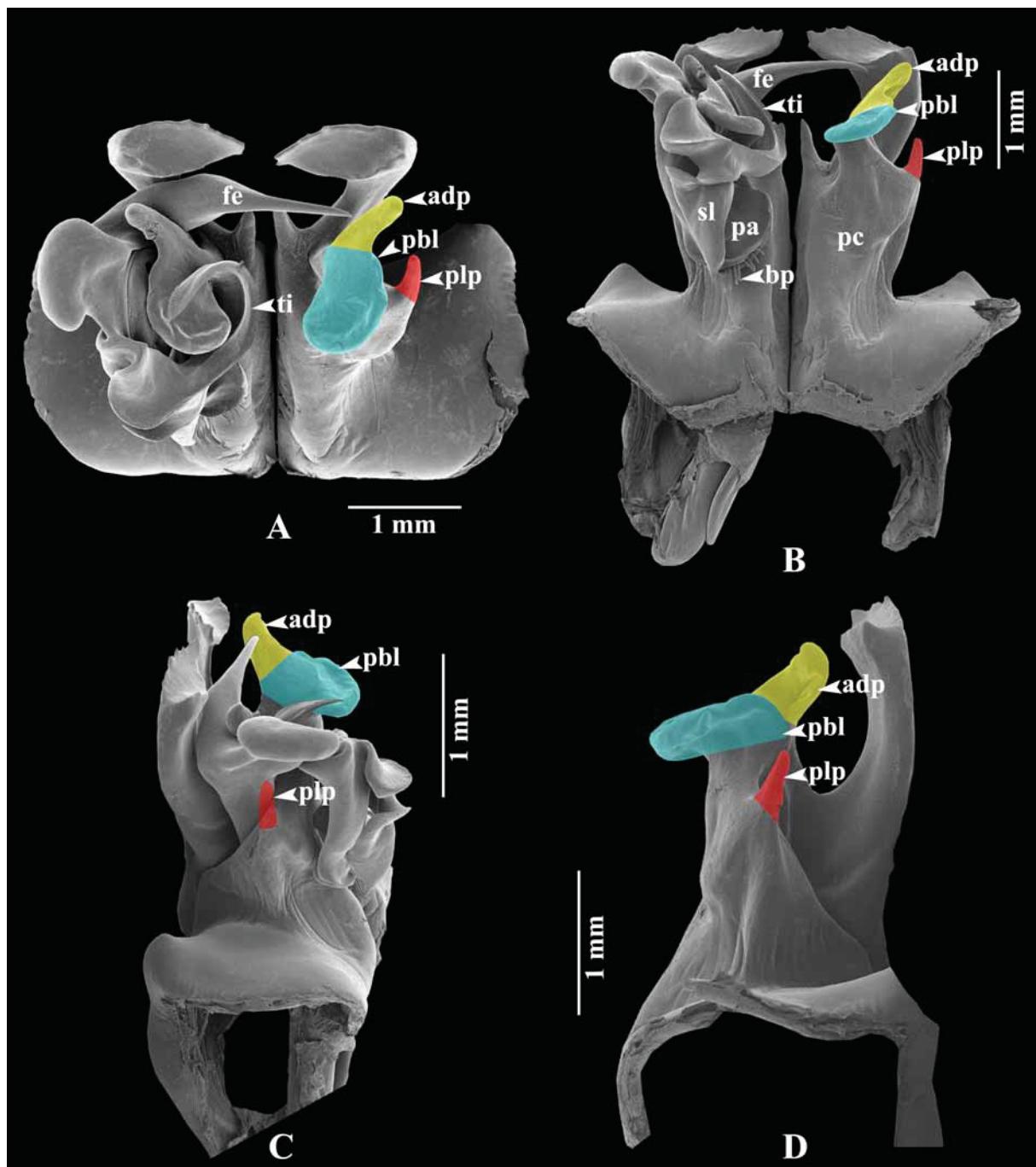
- Anterior coxal fold (*ac*): The main part of the gonopod seen in anterior view. Confusingly called *posterior* coxal fold by Demange (1961) and Hoffman (1975).
- Anterior digitiform process (*adp*): An anterior process originating from *pmp*, normally digitiform.
- Accessory lobe (*al*): A small lamella at the base of the spatulate lobe.
- Lateral process of anterior coxal fold (*alp*): The disto-lateral part of the anterior coxal fold.
- Mesal process of anterior coxal fold (*amp*): An additional projection on the anterior coxal fold, protruding from its mesal margin.
- Blepharochaete (pl. -ae) (*bp*) (Fig. 3): The normal form of apical setae, long, slender, stiffened, and usually pigmented, somewhat reminiscent of the mammalian eyelash (Hoffman, 1975).
- Longitudinal crest in gutter of palette (*cr*): A crest which runs along the middle of the gutter near the tip of the palette.
- Femoral spine (*fe*): A usually long, curved spine on the telopodite, originating slightly distal to the point where the telopodite emerges from the coxa.
- Telopodite lobe (*lo*): A protruding lobe on the telopodite, distal to *fe*.
- Palette (*pa*) (Fig. 3): The distalmost lobe of the apical part, carrying the row of blepharochaetae.
- Posterior broad lobe (*pbl*): A posterior process originating from *pmp*, forming a broad lobe.
- Posterior coxal fold (*pc*): The posterior part of the coxa, usually shorter than *ac* and forming a shelf for accommodation of the telopodite shaft, more or less covered by the telopodite in posterior view. Confusingly called *anterior* coxal fold by Demange (1961) and Hoffman (1975).
- Lateral process of posterior coxal fold (*plp*): The lateral part of the posterior coxal fold, normally digitiform.
- Mesal process of posterior coxal fold (*pmp*): The mesal part of the posterior coxal fold, normally forming a shelf (*sh*) for accommodation of telopodite shaft.
- Paracoxite (*px*): The basal, lateral part of the posterior coxal fold.
- Shelf (*sh*): The distal surface of the posterior coxal fold.
- Spatulate lobe (*sl*) (Fig. 3): A distinct distal separate lobe at the apical part, spatulate, sometimes with a distal spine-like process.
- Small spine (*ss*): An additional small spine at the base of the apical part of the telopodite, visible in posterior view.
- Sternum (*st*): A small, usually triangular sclerite between the basal parts of the anterior coxal folds.
- Tibial spine (*ti*): A usually long spine on the telopodite, originating distal to the femoral spine, at the basis of the apical part of the telopodite, usually curved in the opposite direction of the femoral spine, the two together forming a circle.
- Apical part: The part of the telopodite distal to the tibial spine.



**FIGURE 1.** Semidiagrammatic sketches of *T. allevatus* group gonopod structure labelled according to the terminology employed. A: Gonopods, without telopodites; left = anterior view, right = posterior view. B: telopodite (anterior view). C: telopodite (posterior view).

#### Subgroups of the *T. allevatus* group

Hoffman (1975) mentioned that within the *T. allevatus* group, *T. cuisinieri* and *T. carli* “are distinguished by the exceptionally prominent development of a projecting lobe on the lateral surface of anterior coxal fold [= posterior coxal fold in our terminology]”. These species constitute the ***cuisinieri* subgroup** of the *T. allevatus* group (not to be confused with the “*cuisinieri*-Gruppe” of Attems (1938) which corresponds more or less to the *T. allevatus* group, cf. Hoffman, 1975).



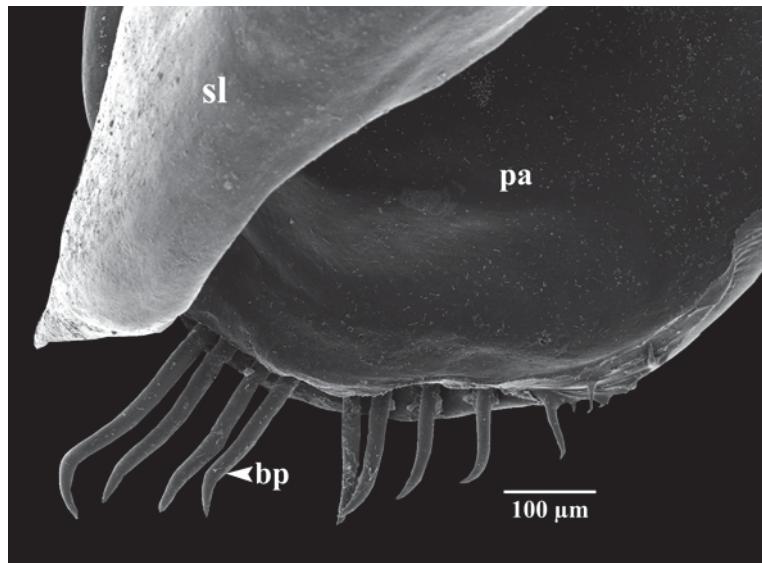
**FIGURE 2.** *Thyropygus implicatus*, SEM. A: apical view, left telopodite removed. B: posterior view, left telopodite removed. C: lateral view, with right telopodite. D: left coxa, lateral view.

A second well-circumscribed subgroup is constituted by the species referred to *Cornugonus* by Demange (1961, 1989) but because we regard it as no more than a subgroup of species with *Thyropygus*, we refer to it as the ***opinatus* subgroup**, *Spirostreptus opinatus* Karsch, 1881, being type species of *Cornugonus*. The *opinatus* subgroup is treated in detail below.

The species transferred to *Cornugonus* by Jeekel (2006), viz. *Thyropisthus bifurcus* Demange, 1986 and *T. enghoffi* Demange, 1989, differ from the *opinatus* subgroup, except *T. cristagalli*, in having a double femoral spine and from all species in the *opinatus* subgroup in lacking a spatulate lobe. They do have a small and slightly folded lateral lamella but this, however, does not form a distinct lobe separated from the apical part of telopodite. These species we place in a third subgroup, the ***bifurcus* subgroup**, which will be the subject of a

forthcoming paper (Pimvichai *et al.* MS).

Further subgroups of the *allevatus* group will be defined in later papers. For the time being, the subgroups should be regarded as purely practical ‘pigeonholes’. At the present stage of analysis, we are unable to assess neither apomorphic vs. plesiomorphic character states, nor the degree of homoplasy. Future analysis of phylogenetic relationships in Harpagophoridae may therefore change the picture dramatically.



**FIGURE 3.** *Thyropygus implicatus*, SEM. Spatulate lobe (sl), palette (pa), blepharochaetae (bp).

### The *opinatus* subgroup

A subgroup of the *Thyropygus allevatus* group, characterized by

1. An additional projection on the anterior coxal fold (very small in *T. loxia* n. sp.)
2. A single femoral spine (exception: *T. cristagalli* n. sp., which has a double femoral spine)
3. An additional apical lobe (the spatulate lobe) on the telopodite

The *opinatus* subgroup includes *T. opinatus* (Karsch, 1881), **n. comb.**, *T. floweri* (Demange, 1961), **n. comb.**, *T. implicatus* (Demange, 1961), **n. comb.**, *T. inflexus* (Demange, 1989), **n. comb.**, and eight new species; *T. bearti* n. sp., *T. bispinispatula* n. sp., *T. bispinus* n. sp., *T. brachyacanthus* n. sp., *T. chelatus* n. sp., *T. cristagalli* n. sp., *T. erectus* n. sp. and *T. loxia* n. sp.

The subgroup is well-defined by the combination of the characters listed above although one, *T. cristagalli*, differs by having a double femoral spine. In this regard, *T. cristagalli* resembles the *T. bifurcus* subgroup, but it differs from this subgroup in having the spatulate lobe on the telopodite. Thus we prefer to classify this species in the *opinatus* subgroup.

In addition to the diagnostic character combination, all species in the *opinatus* subgroup share common characters of head, antennae, mandibles, gnathochilarium, collum, epiproct, paraprocts, hypoproct and first pair of male legs. We therefore give a general description of males of the *opinatus* subgroup, allowing brevity in the subsequent species descriptions.

### General description of the *T. opinatus* subgroup

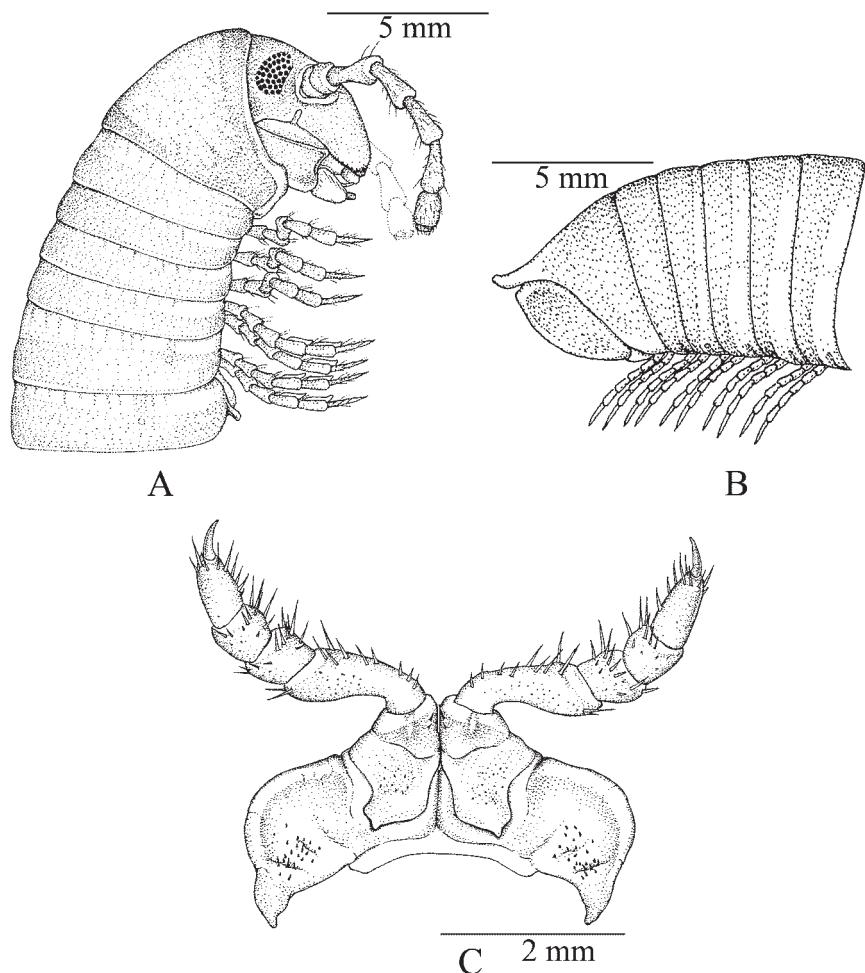
(The description refers to adult males when not otherwise specified)

Head smooth, 5–9 supralabral setae, eyes moderate in size, ocelli in 7–8 horizontal rows: 11–14, 11–13, 9–11,

7–9, 6–8, 4–6, 3–5, 1–4, total: 52–70.

Body rings smooth except for fine longitudinal striation on ventral parts of metazona, ozopores small, situated just behind suture or up to 2 × their diameter behind suture. Sigilla small or medium in size, dispersed over the anterior 1/2–3/4 of metazona.

Antennae (Fig. 4 A) almost reaching back to body ring 3, length of antennomeres: 2>3>4>5>1>6>7.



**FIGURE 4.** *Thropygus chelatus* n. sp., male. A: anterior end. B: posterior end. C: first pair of legs.

Mandibles (Fig. 5): Stipes of male, but not that of female with a poorly sclerotized area on the apical part of the underside.

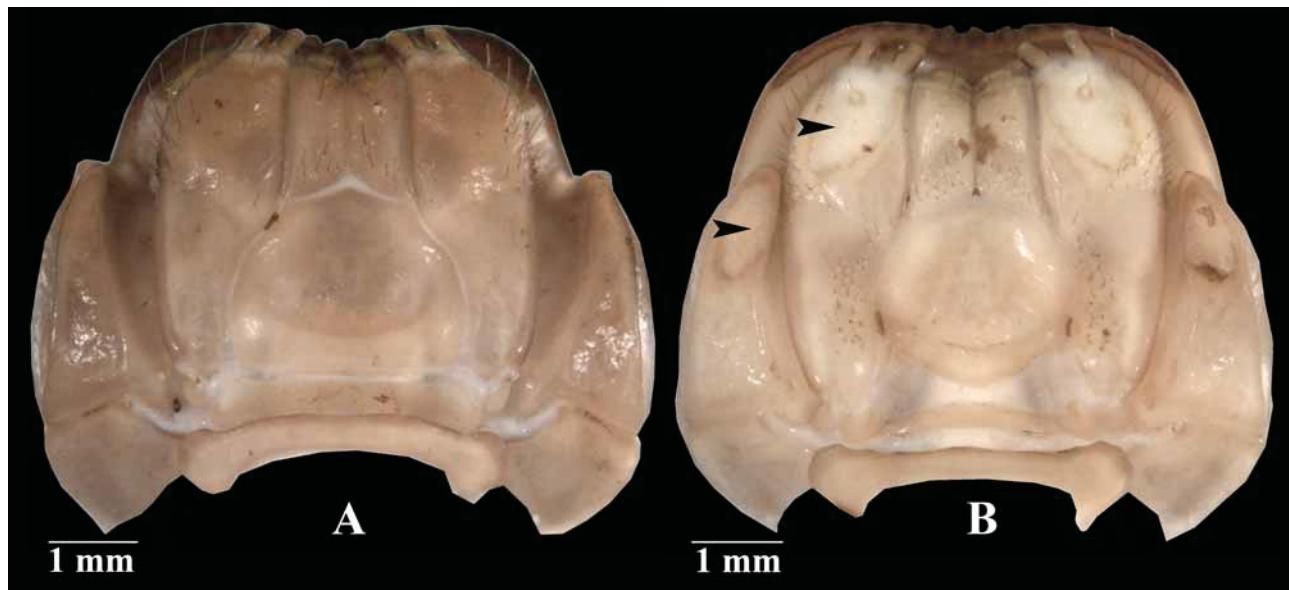
Gnathochilarium (Fig. 5): Mentum smooth, at most with a few small setae distally and a large, horseshoe-shaped ridge opening distally. Stipites densely covered with spine-like setae except for an irregular oblique band from ca. middle of lateral margin to border of lamella lingualis; long setae present on the distal-lateral part; male, but not female distally with an ovoid, poorly sclerotized, hairless area in the middle of which a small sclerotized 'island' carries a single spine-like seta. Lamellae linguale with three long apical setae and a number of short, spine-like ones basally.

Collum (Fig. 4 A) narrowed laterally, ends rounded-truncate, with strong anterolateral maginal groove and ridge.

Epiproct (Fig. 4 B) with a short, upturned dorsal projection. Paraprocts smooth, with rounded and thick valve margins ("lips"). Hypoproct free.

Sterna smooth, stigmatal grooves distinct, long. Legs relatively long; tip of postfemora, tibiae and tarsi visible from above when legs are extended laterad; coxae of anterior and posterior pair markedly dissimilar,

posterior coxae humped; coxae with 1–8 setae, prefemora with 3–7 setae, femora with 2–5 setae in a median row and 2 larger subapical setae; tarsi typically with 6 irregularly placed ventral setae and 1–2 large dorsal apical spurs. Postfemora and tibiae without setae.



**FIGURE 5.** *Thyropygus bearti* n. sp. A: female mandibles and gnathochilarium. B: male mandibles and gnathochilarium. Arrows point at poorly sclerotized areas on right mandibular and gnathochilarial stipites.

First pair of legs (Fig. 4 C) more flattened than the others; sternum a narrow transverse band with a median pointed projection between coxae; coxae broadly expanded, fused in midline, with a field of short setae proximo-laterally; prefemur expanded, without setae, with a blunt triangular projection projecting mesad and slightly anteriad; femur very long, basally very slender; postfemur and tibia shorter than on other legs.

Ventral pads on postfemora and tibiae on all legs except first three pairs.

Gonopods: Sternum (*st*) triangular. Anterior coxal fold (*ac*) basally slender, becoming broader towards tip, lateral margins diverging; distally with two processes: a lateral process (*alp*) and a usually smaller mesal process (*amp*); the shape of these processes is species-specific. Posterior coxal (*pc*) fold much lower than anterior coxal fold, basally with moderately high lateral paracoxites (*px*), distally variously modified (Fig. 2A–D) but always with a smooth area over which the telopodite shaft can slide. Telopodite with a single, well-developed femoral spine (*fe*) (with a doubled femoral spine in *T. cristagalli*) and a long, slender, curved tibial spine (*ti*). A characteristic spatulate lobe (*sl*) originating under the base of the tibial spine; lobe sometimes distally rounded, spoon-like, sometimes ending in a large, stout spine (two spines in *T. bispinispatula*). Apical palette (*pa*) simple, forming a broad gutter, sometimes with a longitudinal crest in the concavity; apically with a row of 7–13 brownish blepharochaetae (*bp*).

#### Key to species of the *T. opinatus* subgroup

- 1 Spatulate lobe (*sl*) distally drawn out into one (rarely two) sharp dark brown spine(s). . . . . 2
- 1\* Spatulate lobe (*sl*) distally expanded and/or rounded, spoonlike, without a spine . . . . . 6
- 2 Spatulate lobe (*sl*) terminating in two sharp brown spines, the outer spine slightly smaller and shorter than the inner one; lateral process of anterior coxal fold (*alp*) slender, slightly curving mesad; mesal process of anterior coxal fold (*amp*) almost as long as *alp*, flattened. . . . . *Thyropygus bispinispatula* n. sp.
- 2\* Spatulate lobe (*sl*) terminating in a single sharp dark brown spine . . . . . 3
- 3 Telopodite distally to *fe* with a large, round lobe (*lo*) projecting distolaterally . . . . . 4
- 3\* Telopodite without a lobe distal to *fe*; lateral process of anterior coxal fold (*alp*) long, slender, regularly curved, tip

close to tip of opposite *alp*, the two together forming a circle; mesal process of anterior coxal fold (*amp*) straight, shorter than *alp*; femoral spine (*fe*) directed distad, pointed..... *Thyropygus erectus* n. sp.

4 Lateral process of anterior coxal fold (*alp*) very slender, regularly curved, simple, tip close to tip of the opposite side, the two together forming a circle; mesal process of posterior coxal fold (*pmp*): strongly developed along anterior-posterior axis..... *Thyropygus floweri* (Demange, 1961) n. comb.

4\* Lateral process of anterior coxal fold (*alp*) different, broader and/or with several apical denticles ..... 5

5 Lateral process of anterior coxal fold (*alp*) broad, apically gradually narrowed; mesal process of anterior coxal fold (*amp*) almost as long as lateral process (*alp*), slender, straight, terminally slightly curved, pointed ..... *Thyropygus opinatus* (Karsch, 1881) n. comb.

5\* Lateral process of anterior coxal fold (*alp*) apically bent abruptly mesad, tip with serrate margins; mesal process of anterior coxal fold (*amp*) much shorter than lateral process (*alp*), directed meso-distad, simple, pointed; mesal process of posterior coxal fold (*pmp*): strongly developed along anterior-posterior axis..... *Thyropygus implicatus* (Demange, 1961) n. comb.

6 Lateral process of anterior coxal fold (*alp*) broad, mesal margin concave, tip with serrate margins, cockscomb-like; mesal process of anterior coxal fold (*amp*) much shorter than lateral process (*alp*), directed meso-distad, simple, pointed; an additional spine-like process (*aip*) between *alp* and *amp* ..... *Thyropygus cristagalli* n. sp.

6\* Lateral process of anterior coxal fold (*alp*) slender, regularly curved, no additional process between lateral (*alp*) and mesal (*amp*) ones ..... 7

7 Lateral process of anterior coxal fold (*alp*) apically abruptly truncate..... *Thyropygus bearti* n. sp.

7\* Lateral process of anterior coxal fold (*alp*) apically pointed ..... 8

8 Mesal process of anterior coxal fold (*amp*) very small, telopodite distally to *fe* with a small round lobe (*lo*) projecting distolaterally..... *Thyropygus loxia* n. sp.

8\* Mesal process of anterior coxal fold (*amp*) relatively long ..... 9

9 Mesal process of anterior coxal fold (*amp*) much shorter than lateral process (*alp*), directed obliquely disto-mesad, slender, straight ..... *Thyropygus chelatus* n. sp.

9\* Mesal process of anterior coxal fold (*amp*) directed distad, thicker, straight or slightly sigmoid ..... 10

10 Mesal process of anterior coxal fold (*amp*) almost as long as lateral process (*alp*), slightly sigmoid, pointed; mesal process of posterior coxal fold (*pmp*) directed distolaterad..... *Thyropygus brachyacanthus* n. sp.

10\* Mesal process of anterior coxal fold (*amp*) longer than lateral process (*alp*), directed distad, parallel with opposite process ..... 11

11 Lateral process of anterior coxal fold (*alp*) apically with a crest extending caudad and ending in a small spine; mesal process of anterior coxal fold (*amp*) apically irregularly tuberculate; telopodite distally without a rounded lobe (*lo*); femoral spine (*fe*) short; spatulate lobe (*sl*) distally rounded, with smooth edges..... *Thyropygus inflexus* (Demange, 1989) n. comb.

11\* Lateral process of anterior coxal fold (*alp*) apically without a crest; mesal process of anterior coxal fold (*amp*) apically sharp; telopodite distally with a rounded lobe (*lo*); femoral spine (*fe*) long; margins of spatulate lobe (*sl*) terminally meeting in a distinct angle ..... *Thyropygus bispinus* n. sp.

## Species descriptions

### *Thyropygus opinatus* (Karsch, 1881), n. comb.

(Figs. 6A–F, 18A)

*Spirostreptus opinatus* Karsch, 1881: 23

*Spirostreptus opinatus*: Pocock 1889: 294, 1893: 401

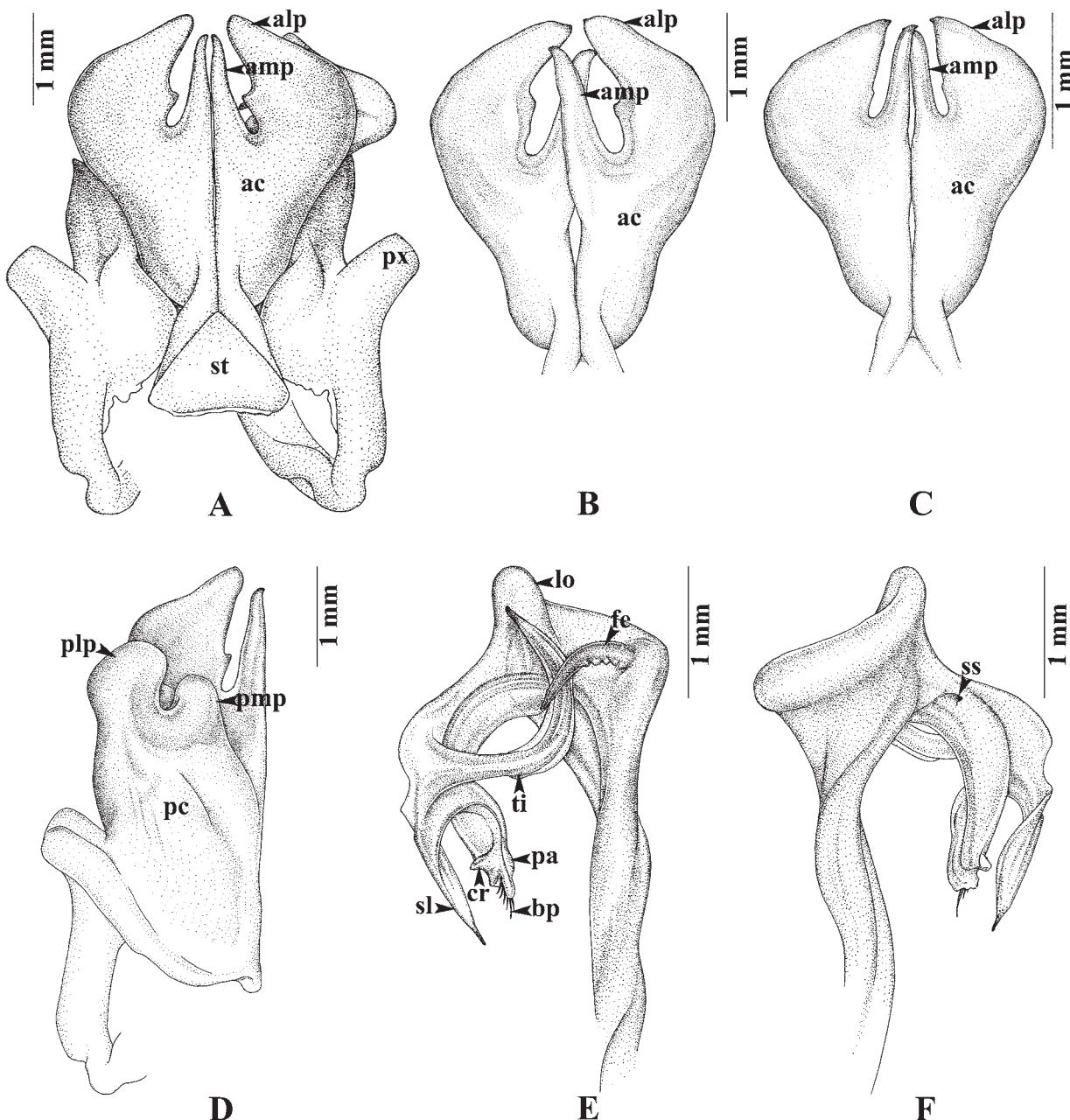
*Spirostreptus regis* Pocock, 1889: 297 (?)

*Spirostreptus andersoni* Pocock, 1893: 401 (nomen nudum?) (?)

*Cornugonus opinatus*: Demange, 1961: 178

**Material:** 1 male MYANMAR, Malewoon, 10° 14' 0" N, 98° 37' 0" E. Fea leg., (ZMUC). This specimen comes from the same series as that illustrated by Demange (1961), studied earlier by Pocock (1893) and now belonging to MNHN, 3 males, 2 females THAILAND, Petchaburi Province, Cha-Um district, at Nakwang cave, 12° 51' 26" N, 99° 56' 29" E. 6 October 2008. H. Enghoff, S. Panha, P. Pimvichai and members of Animal Systematics Research Unit leg., (CUMZ), 1 male THAILAND, Prachuap Khirikhan Province, Bang Saphan district, Ban Grude, 11° 16' 25" N, 99° 33' 1" E. 12 October 2008. C. Sutcharit and P. Tongkerd leg.,

(CUMZ), 3 males THAILAND, Prachuap Khirikhan Province, Khao Sam Roi Yot National Park, ca. 100 m before Kaeo cave, 12° 11' 17" N, 99° 59' 27" E. 21 July 2006. G. Hantke & F. Brand leg., (SMF) and 4 males THAILAND, Prachuap Khirikhan Province, Khao Sam Roi Yot National Park, ca. surrounding of 10 m from Kaeo cave, 12° 12' 6" N, 99° 59' 25" E. 22 July 2006. G. Hantke & F. Brand leg., (SMF, ZMUC)



**FIGURE 6.** (A, D, E, F): *Thyropygus opinatus*, gonopods. A: anterior view, left telopodite removed (specimen from Malewoon). B: anterior view, anterior coxal fold (specimen from Nakwang cave). C: anterior view, anterior coxal fold (specimen from Ban Krude). D: right coxa, posterior view. E: right telopodite, anterior view. F: right telopodite, posterior view.

**Diagnosis:** A species of the *opinatus* subgroup. Spatulate lobe (*sl*) at apical part of telopodite terminating in a sharp brown spine. Similar in this respect to *T. floweri*, *T. implicatus* and *T. erectus*. Differing from these species by mesal margin of anterior coxal fold (*alp*) serrated or with a single denticle, with a small spine (*ss*) at base of apical part, opposite the origin of tibial spine, and the mesal process of anterior coxal fold (*amp*) almost as long as lateral process.

**Description:** Adult males with 62–70 podous rings, no apodous rings. Length ca. 19–21 cm, width ca. 10.5–11.5 mm. Adult females with 70 podous rings, no apodous rings. Length ca. 18 cm, width ca. 9.8–10.8 mm. Overall color of living animal (Fig. 18A) black. Legs and antennae reddish brown. Epiproct and margins of paraprocts yellowish brown.

Gonopods (Figs. 6A–F): Anterior coxal fold (*ac*): lateral process (*alp*) broadly expanded and apically gradually narrowed, mesal margin with fine serrations (Demange 1961: fig. 244) or smooth with a single denticle (Figs. 6A–C, Pocock 1889: fig. 2b); mesal process (*amp*) almost as long as lateral process, slender, straight, directed distad, terminally slightly curved, pointed, sometimes crossing over with opposite *amp* (Figs. 6A–C). Posterior coxal fold (*pc*) (Fig. 6D) distally with two processes: mesal process (*pmp*) a rounded lobe, shorter than lateral process (*plp*) and separated from *plp* by deep, rounded sinus; lateral process (*plp*) a large, smooth, rounded node, projecting further caudad than mesal process. Telopodite (Figs. 6E–F): Femoral spine (*fe*) long, slender, very distinctly crenulated along outer curvature, *in situ* resting against posterior surface of *alp*; telopodite distally to *fe* with a massive, broad, round lobe (*lo*) projecting distolaterally; tibial spine (*ti*) long, slender, recurved, in anterior view crossing over with *fe* and reaching mesal end of *lo*; apical part: spatulate lobe (*sl*) terminating in a sharp brown spine (very slender in Nakwang specimens); a small spine (*ss*) at base of apical part, opposite the origin of *ti*; palette (*pa*) simple, with a longitudinal rounded crest (*cr*) near tip, distally with about ten brownish blepharochaetae (*bp*).

**Distribution** (Fig. 20): Described from MYANMAR, Tenasserim, without an exact locality (Karsch, 1881). Subsequently recorded from Sullivan Island ( $10^{\circ} 50' 0''$  N,  $98^{\circ} 15' 0''$  E) by Pocock (1889). The Myanmar specimens studied by us, Pocock (1893) and Demange (1961) are from Malewoon, Tenasserim ( $10^{\circ} 14' 0''$  N,  $98^{\circ} 37' 0''$  E). We here record the species as new to Thailand based on specimens from Petchaburi and Prachuap Khirikhan Provinces. The records from King Island (Pocock 1889), and from "S. Tenasserim" (Pocock, 1893) are fraught with serious doubts (see notes) and are not shown on the map.

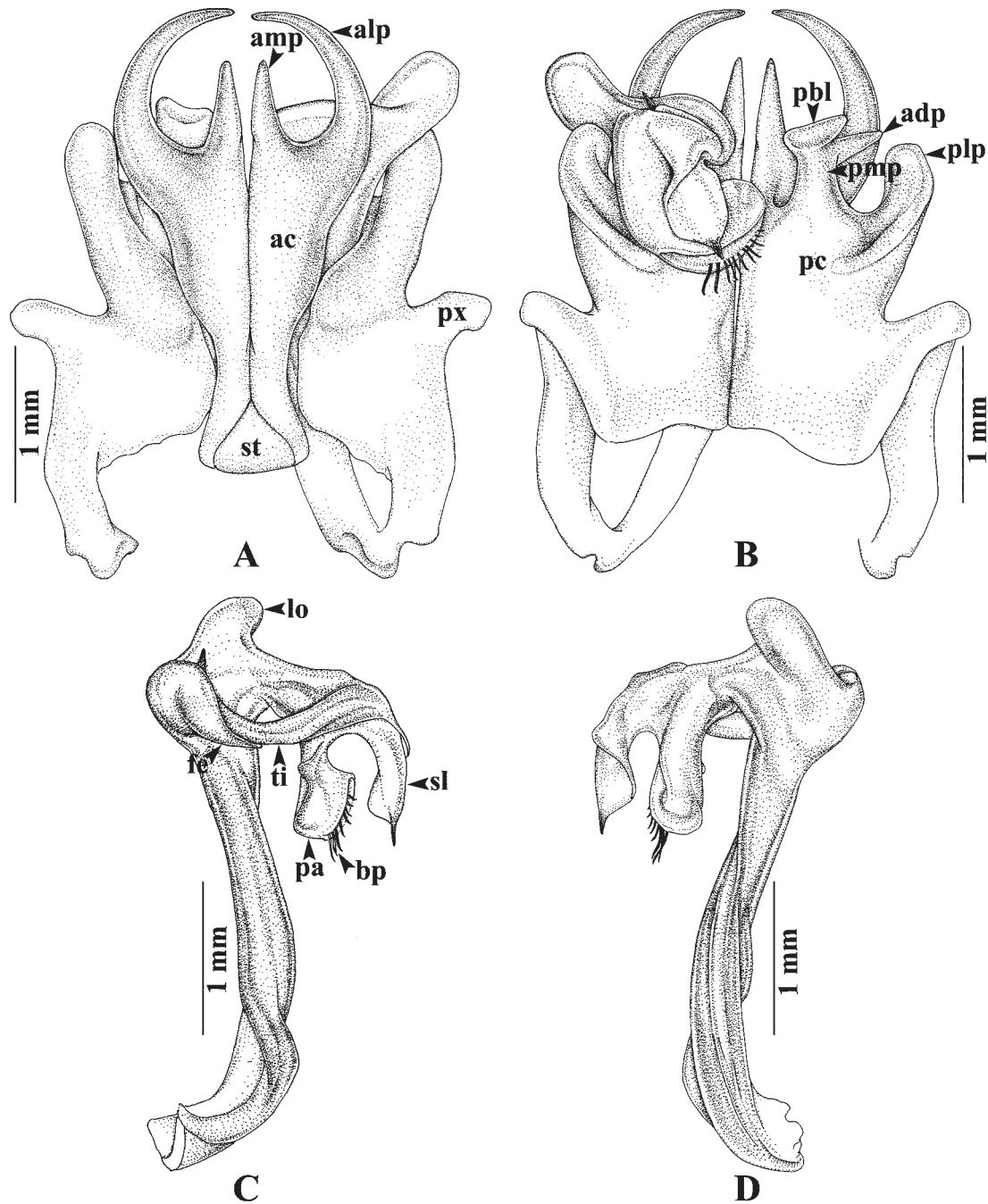
**Notes:** This species presents several unresolved problems. The original description (Karsch, 1881) was said to be based on a male, but as usual, Karsch did not describe the gonopods. The whereabouts of the type specimen are unknown. The next mention of *opinatus* was by Pocock (1889) who reported it from Sullivan Island. Pocock gave a relatively good description, including a small gonopod drawing. In 1893, Pocock recorded *opinatus* from Malewoon and further noted that "Two young examples collected by Oates in S. Tenasserim are doubtfully referred to this species" and further that "This species was originally described from Tenasserim and was subsequently procured by Dr. Anderson from the Mergui Archipelago". The latter statement must refer to the name "? *Sp. andersoni*" Pocock, 1889 listed in the synonymy of *opinatus* by Pocock (1893) with an exact reference to the page and figure number in his 1889 paper and a note that this name is based on a young specimen. The strange thing is that in Pocock (1889) there is no *Spirostreptus andersoni*; instead there is, on the cited page and under the cited figure number, a *Spirostreptus regis* Pocock, 1889, based on a single female from King Island. The length of this specimen was given as 55 mm which does suggest a juvenile. It seems most likely that *andersoni* is a *lapsus calami* for *regis*, maybe due to confusion with *Spirobolus andersoni* Pocock, 1889, described just two pages after *Spirostreptus regis*. Demange (1960) found specimens of neither *andersoni* nor *regis* in the Natural History Museum of London.

Demange (1961) based his description of *opinatus* on a specimen from Malewoon examined by Pocock (1893), and we have carried on this understanding of *opinatus*, being aware that rediscovery of Karsch's type specimen may require a revision. Pocock's (1889) gonopod drawing based on the specimen he described from Sullivan Island bears a strong resemblance to our Fig. 6A, although the lateral process (*alp*) of the anterior gonopod fold looks slightly narrower in the Sullivan Island specimen. Considering that the specimen illustrated by Demange (1961) is again slightly different from the one from the same series studied by us, in this case with an even broader *alp*, and further considering the variability among the new Thai specimens, we accept the record of *opinatus* by Pocock (1889) as belonging to this species as understood here.

*Thyropygus floweri* (Demange, 1961), n. comb.  
(Figs. 7A–D)

*Cornugonus floweri* Demange, 1961: 184. Holotype (not seen) in the Natural History Museum, London.

**Material:** 1 male THAILAND, Yala Province, Bang Lang National Park,  $6^{\circ} 04' 12''$  N,  $101^{\circ} 11' 18''$  E. 19 October 1991. M. Andersen, O. Martin and N. Scharff leg., (ZMUC).



**FIGURE 7.** *Thyropygus floweri*, specimen from Bang Lang National Park, gonopods. A: anterior view, left telopodite removed. B: posterior view, left telopodite removed. C: left telopodite, anterior view. D: left telopodite, posterior view.

**Diagnosis:** A species of the *opinatus* subgroup. Spatulate lobe (*sl*) at the apical part of telopodite terminating in a sharp brown spine. Similar in this respect to *T. opinatus*, *T. implicatus* and *T. erectus*. Differs from the first two of these species by the lateral process of anterior coxal fold (*alp*) being very slender and

regularly curved, the two *alp*'s forming a circle. Particularly similar to *T. erector*, but differing from it by having the mesal process of anterior coxal fold (*amp*) much shorter than *alp*, by having the mesal process of posterior coxal fold (*pmp*), strongly developed along the anterior-posterior axis, and by the presence of a telopodite lobe (*lo*).

**Description:** Adult male with 62 podous rings, no apodous rings. Length ca. 12 cm, width ca. 8.0 mm. Color in life unknown; preserved specimen with prozona whitish-brown, metazona, tip of epiproct, paraprocts, and tip of hypoproct dark brown, head, antennae, middorsal metazona, legs, epiproct and hypoproct brown.

Gonopods (Figs. 7A–D): Anterior coxal fold (*ac*) (Fig. 7A): lateral process (*alp*) long, slender, regularly curved, tip close to tip of opposite *alp*, the two together forming a circle; mesal process (*amp*) much shorter than *alp*, straight, directed distad. Posterior coxal fold (*pc*) (Fig. 7B) with lateral paracoxites (*px*) digitiform; mesal process (*pmp*): strongly developed along anterior-posterior axis, with a large broad, somewhat hammer-shaped lobe (*pbl*) curving caudad, and an anterior slender digitiform process (*adp*). Telopodite (Figs. 7C–D) leaving coxite in front of *adp*; femoral spine (*fe*) massive, curving mesad in the horizontal plane and resting against posterior surface of *ac*; telopodite distally to *fe* with a large, round lobe (*lo*) projecting distolaterally; tibial spine (*ti*) very long, slender, curving under *pbl* in horizontal plane, its tip upturned and resting against anterior surface of *adp*; apical part: spatulate lobe (*sl*) with a sharp dark brown spine at tip; palette (*pa*) simple, distally with about ten brownish blepharochaetae (*bp*).

**Distribution** (Fig. 20): Described from MALAYSIA, Bukit Jalor, (Demange, 1961), based on a specimen belonging to the Natural History Museum in London. This locality was part of Malaysia in the past but now Jalor belongs to THAILAND, and the name has changed to Yala. The specimen studied by us, collected in Yala Province, Bang Lang National Park, may thus be a topotype. The species was recorded as new for the Thai fauna by Enghoff (2005) based on this specimen and for the time being should be regarded as a Thai endemic.

### *Thyropygus implicatus* (Demange, 1961), n. comb.

(Figs. 2, 3, 8A–D)

*Cornugonus implicatus* Demange, 1961: 181. Holotype (not seen) in the Natural History Museum, London.

**Material:** 10 males, 5 females, and 1 juvenile THAILAND, Satun Province, Thale Ban National Park, 6° 42' 29" N, 100° 10' 46" E. 15 October 1991. M. Andersen, O. Martin and N. Scharff leg., (ZMUC).

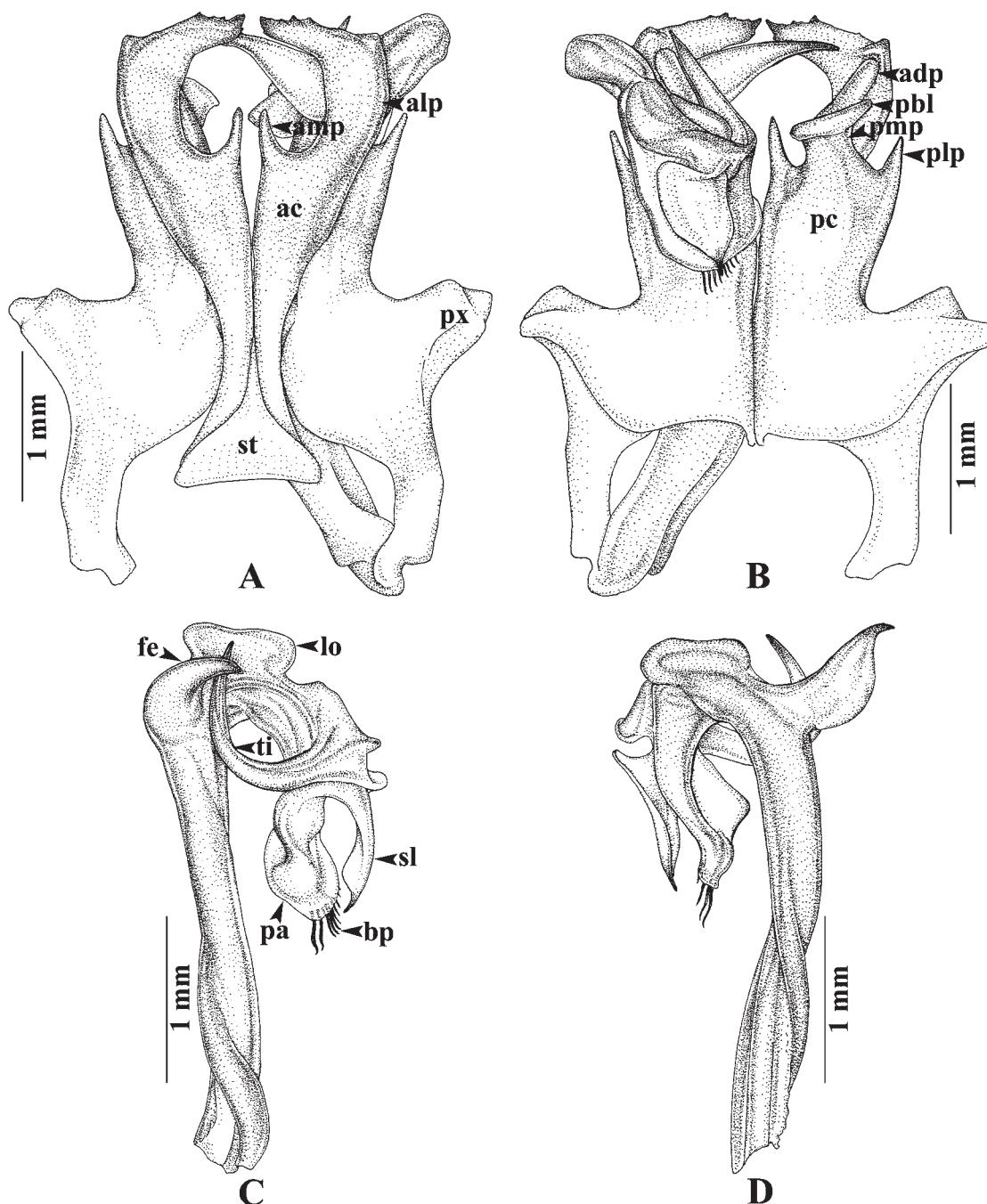
**Diagnosis:** A species of the *opinatus* subgroup. Spatulate lobe (*sl*) at the apical part of telopodite terminating in a sharp brown spine. Similar in this respect to *T. opinatus*, *T. floweri* and *T. erector*. Differs from these species by the having the lateral process of the anterior coxal fold (*alp*) apically bent abruptly mesad, its tip with serrate margins.

**Description:** Adult males with 63–70 podous rings, no apodous rings. Length ca. 12–13 cm, width ca. 7.4–8.0 mm. Adult females with 65–80 podous rings, no apodous rings. Length ca. 12–22 cm, width ca. 8.0–11.0 mm. Color in life unknown; preserved specimens with head, antennae, legs, prozona, middorsal metazona, epiproct, paraprocts and hypoproct brown; metazona, margins of epiproct and paraprocts, and the tip of hypoproct darker brown.

Gonopods (Figs. 8A–D): Anterior coxal fold (*ac*) (Fig. 8A): lateral process (*alp*) apically bent abruptly mesad, tip with serrate margins, posterior side with a horizontal crest; mesal process (*amp*) much shorter than lateral process, directed meso-distad, pointed. Posterior coxal fold (*pc*) (Fig. 8B) with lateral paracoxites (*px*), digitiform; mesal process (*pmp*) complex, strongly developed along an anterior-posterior axis, with a large posterior broad lobe (*pbl*) and an anterior slender digitiform process (*adp*); lateral process (*plp*) small, pointed. Telopodite (Figs. 8C–D) leaving coxite between *pmp* and *plp*; femoral spine (*fe*) basally massive, ending in sharp point, directed almost straightly mesad, *in situ* resting against posterior surface of *alp*, fitting

under its horizontal crest, crossing over with *fe* of the opposite side; telopodite distally to *fe* with a large, round lobe (*lo*) projecting distolaterally; tibial spine (*ti*) long, slender, curving in horizontal plane, its tip upturned and resting against anterior surface of *adp*; apical part: spatulate lobe (*sl*) terminating in a sharp brown spine; palette (*pa*) simple, gutter-like, distally with about nine brownish blepharochaetae (*bp*).

**Distribution** (Fig. 20): Described from MALAYSIA, Penang Hill ( $5^{\circ} 25' 29''$  N,  $100^{\circ} 16' 7''$  E) (Demange, 1961), based on specimens (including holotype) belonging to the Natural History Museum in London, and further specimens from MALAYSIA, Malacca, Sultanate of Kedah ( $2^{\circ} 27' 16''$  N,  $102^{\circ} 25' 47''$  E) belonging to Naturalis, Leiden. The species was recorded as new for the Thai fauna by Enghoff (2005) based on the specimens studied by us (THAILAND, Satun Province, Thale Ban National Park).

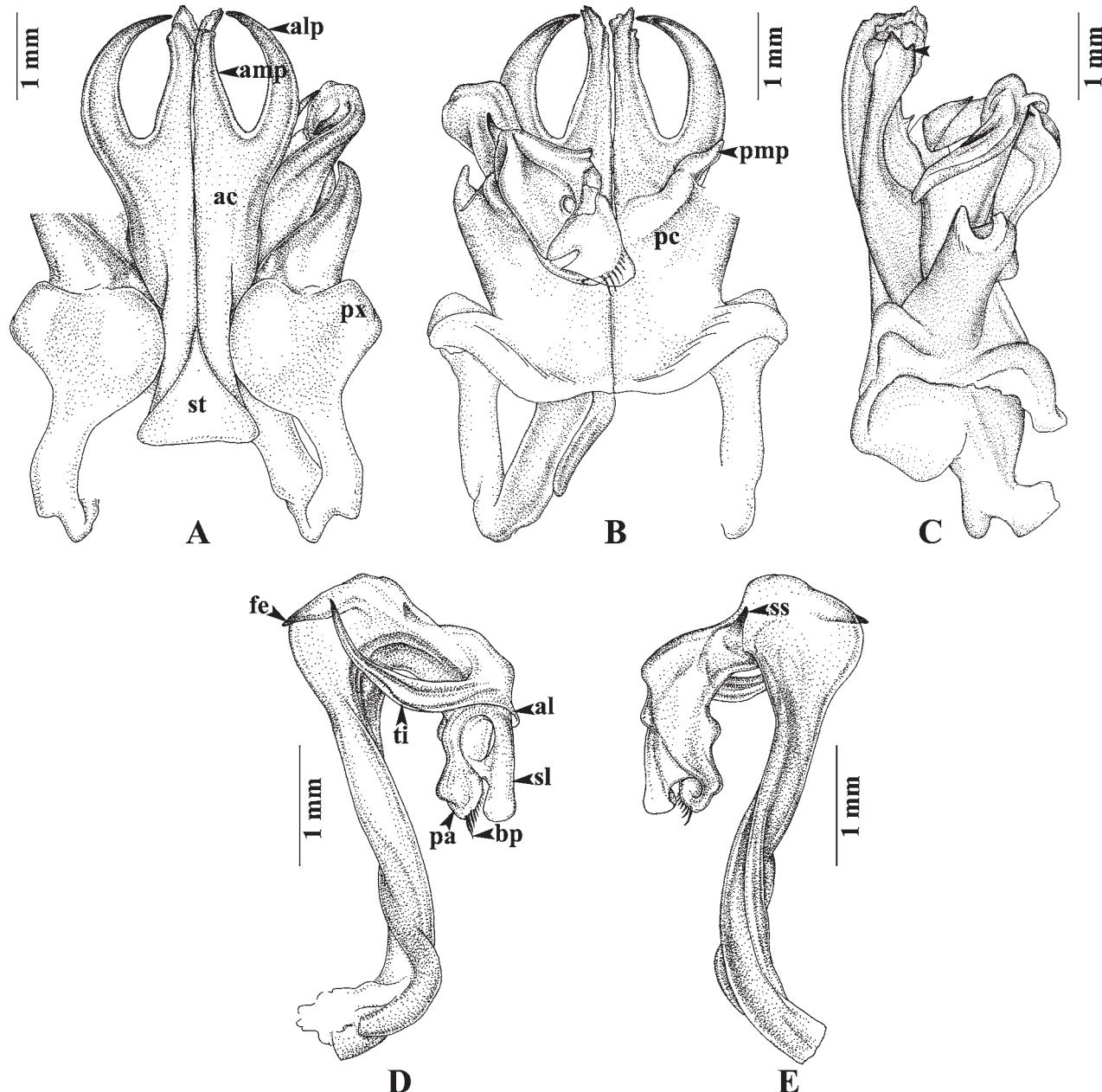


**FIGURE 8.** *Thyropygus implicatus*, specimen from Thale Ban National Park, gonopods. A: anterior view, left telopodite removed. B: posterior view, left telopodite removed. C: left telopodite, anterior view. D: left telopodite, posterior view.

***Thyropygus inflexus* (Demange, 1989), n. comb.**  
 (Figs. 9A–E)

*Cornugonus inflexus* Demange, 1989: 780

**Material:** HOLOTYPE male THAILAND, Kanchanaburi Province, Sai Yok district, 14° 6' 56" N, 99° 8' 40" E. 16 June 1986. L. Deharveng leg., (MNHN).



**FIGURE 9.** *Thyropygus inflexus*, holotype, gonopods. A: anterior view, left telopodite removed. B: posterior view, left telopodite removed. C: lateral view. D: left telopodite, anterior view. E: left telopodite, posterior view.

**Diagnosis:** A species of the *opinatus* subgroup. Spatulate lobe (*sl*) at the apical part of telopodite expanded, smooth and without a spine. Similar in this respect to *T. bearti*, *T. chelatus*, *T. cristagalli*, *T. brachyacanthus*, *T. loxia* and *T. bispinus*. Differs from the first five of these species by the mesal process of the anterior coxal fold (*amp*) being longer than the lateral process of anterior coxal fold (*alp*). Particularly

similar to *T. bispinus*, differing from it by *alp* apically with a crest extending caudad and ending in a small spine (Fig. 9C, arrow), *amp* apically irregularly tuberculate, the absence of telopodite lobe (*lo*), and having a small spine (*ss*) at base of apical part, opposite the origin of tibial spine.

**Description:** Adult male with 69 podous rings, no apodous rings. Length ca. 13 cm (broken), width ca. 7.0 mm. Color in life unknown; preserved specimen with prozona, epiproct, and paraprocts whitish-brown, Head, antennae, legs, metazona, tip of epiproct, margins of paraprocts, and hypoproct brown.

Gonopods (Figs. 9A–E): Anterior coxal fold (*ac*) (Fig. 9A): lateral process (*alp*) long, slender, regularly curved, in anterior view sickle-shaped, apically with a crest extending caudad and ending in a small spine (Fig. 9C, arrow); mesal process (*amp*) slightly longer than lateral process (*alp*), protruding from middle of mesal margin of *ac*, apically irregularly tuberculate. Posterior coxal fold (*pc*) (Fig. 9B) basally with moderately high lateral paracoxites (*px*); mesal process (*pmp*) slender, directed distolaterad; lateral process (*plp*) damaged on both sides of unique specimen. Telopodite (Figs. 9D–E): Femoral spine (*fe*) flattened, short, lying close to top of telopodite; tibial spine (*ti*) very long, curving in horizontal plane; spatulate lobe (*sl*) basally slender, distally broadly expanded, with inner lateral margin arched; a small accessory lobe (*al*) at base of *sl*; and a small slender spine (*ss*) at base of apical part, opposite the origin of the tibial spine; palette (*pa*) simple, gutter-like, distally with about seven brownish blepharochaetae (*bp*).

**Distribution** (Fig. 20): Described from THAILAND, Kanchanaburi [Kanchanaburi], without an exact locality (Demange, 1989). The more precise locality of the holotype, which is the only known specimen, is Kanchanaburi Province, Sai Yok district (L. Deharveng, personal communication).

### *Thyropygus bearti* n. sp.

(Figs. 5, 10A–D, 18B)

**Material:** HOLOTYPE male THAILAND, Suratthani Province, Don Sak district, Khao Sai, 9° 14' 48" N, 99° 45' 51" E. 27 August 2007. H. Enghoff and S. Panha leg., (CUMZ). – Paratypes: 1 female, same data as holotype (CUMZ), 1 male, 1 female, same data as holotype (ZMUC).

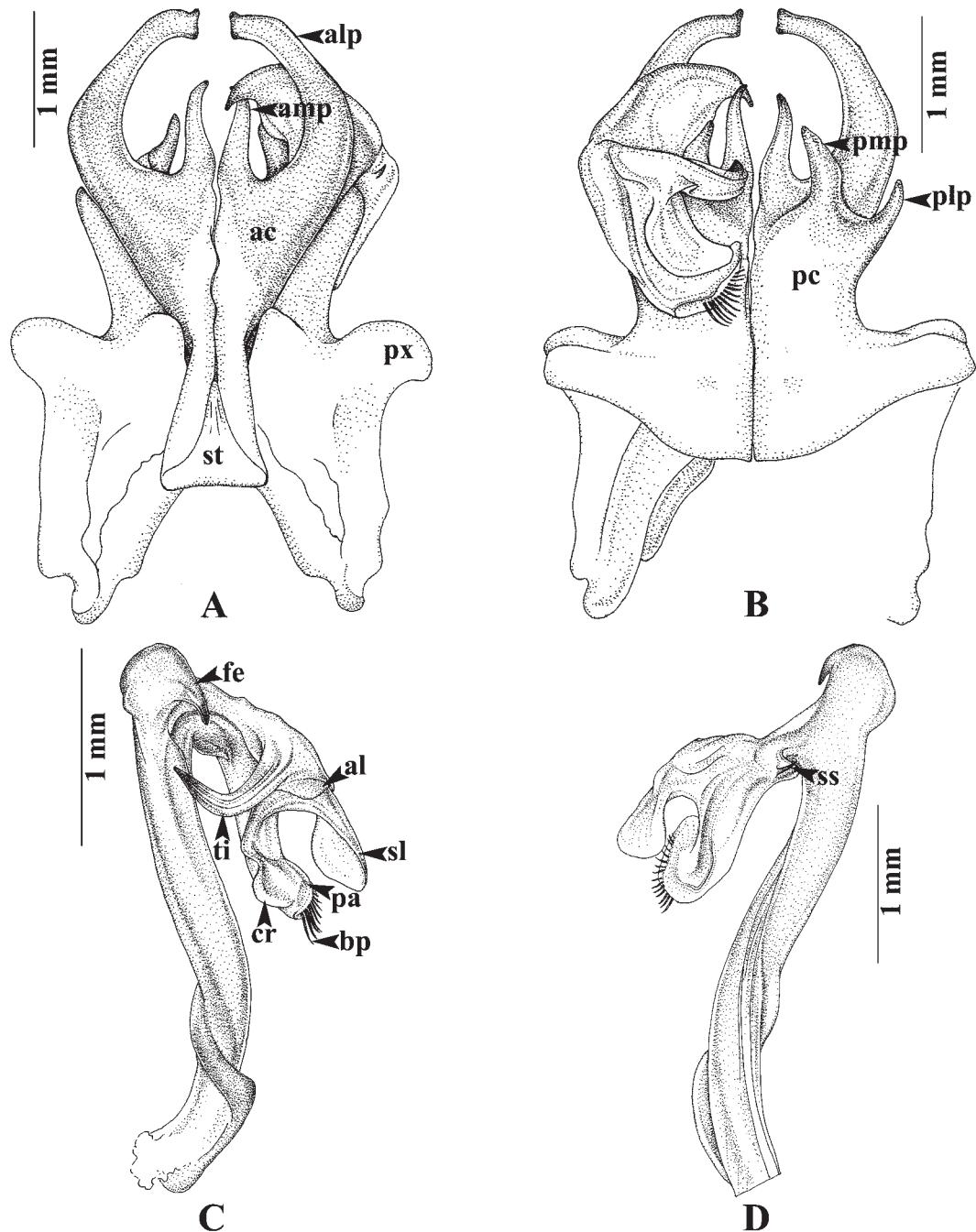
**Etymology:** The species is named after the Thai Biodiversity Research and Training Program (BRT), in recognition of this agency's support for our research.

**Diagnosis:** A species of the *opinatus* subgroup. Spatulate lobe (*sl*) at the apical part of telopodite rounded, spoon-like. Similar in this respect to *T. inflexus*, *T. chelatus*, and *T. cristagalli*, *T. brachyacanthus* and *T. loxia*. Differs from these species by the apical palette (*pa*) having a longitudinal rounded crest near tip, and by the lateral process of anterior coxal fold (*alp*) being apically abruptly truncate.

**Description:** Adult males with 61–62 podous rings, no apodous rings. Length ca. 12–13 cm, width ca. 7.4 mm. Adult females with 62–63 podous rings, no apodous rings. Length ca. 12 cm, width ca. 7.6–7.8 mm. Overall color of living animal (Fig. 18B) brown. Legs and antennae pink, prozona, head, epiproct, paraprocts, and hypoproct brown, metazona pinkish brown.

Gonopods (Figs. 10A–D): Anterior coxal fold (*ac*) (Fig. 10A): lateral process (*alp*) slightly curved, directed obliquely mesad, apically abruptly truncate; mesal process (*amp*) much shorter than lateral process, directed distad, slightly sigmoid, pointed. Posterior coxal fold (*pc*) (Fig. 10B) basally with moderately high paracoxites (*px*), distally with two processes: mesal process (*pmp*) pointed-triangular, directed almost straightly distad; lateral process (*plp*) much shorter, digitiform, directed distad and slightly laterad. Telopodite (Figs. 10C–D) leaving coxite between *pmp* and *plp*; femoral spine (*fe*) basally very broad, curving mesad and ending in sharp point; tibial spine (*ti*) long, slender, curving in horizontal plane, its tip *in situ* resting between *pmp* and *amp*; apical part: spatulate lobe (*sl*) basally slender, distally expanded, rounded, spoon-like; a small accessory lobe (*al*) at base of *sl*; and a small slender spine (*ss*) at base of apical part, opposite the origin of *ti*; palette (*pa*) simple, gutter-like, with a longitudinal rounded crest (*cr*) near tip, distally with about thirteen brownish blepharochaetae (*bp*).

**Distribution** (Fig. 20): Known only from the type locality.



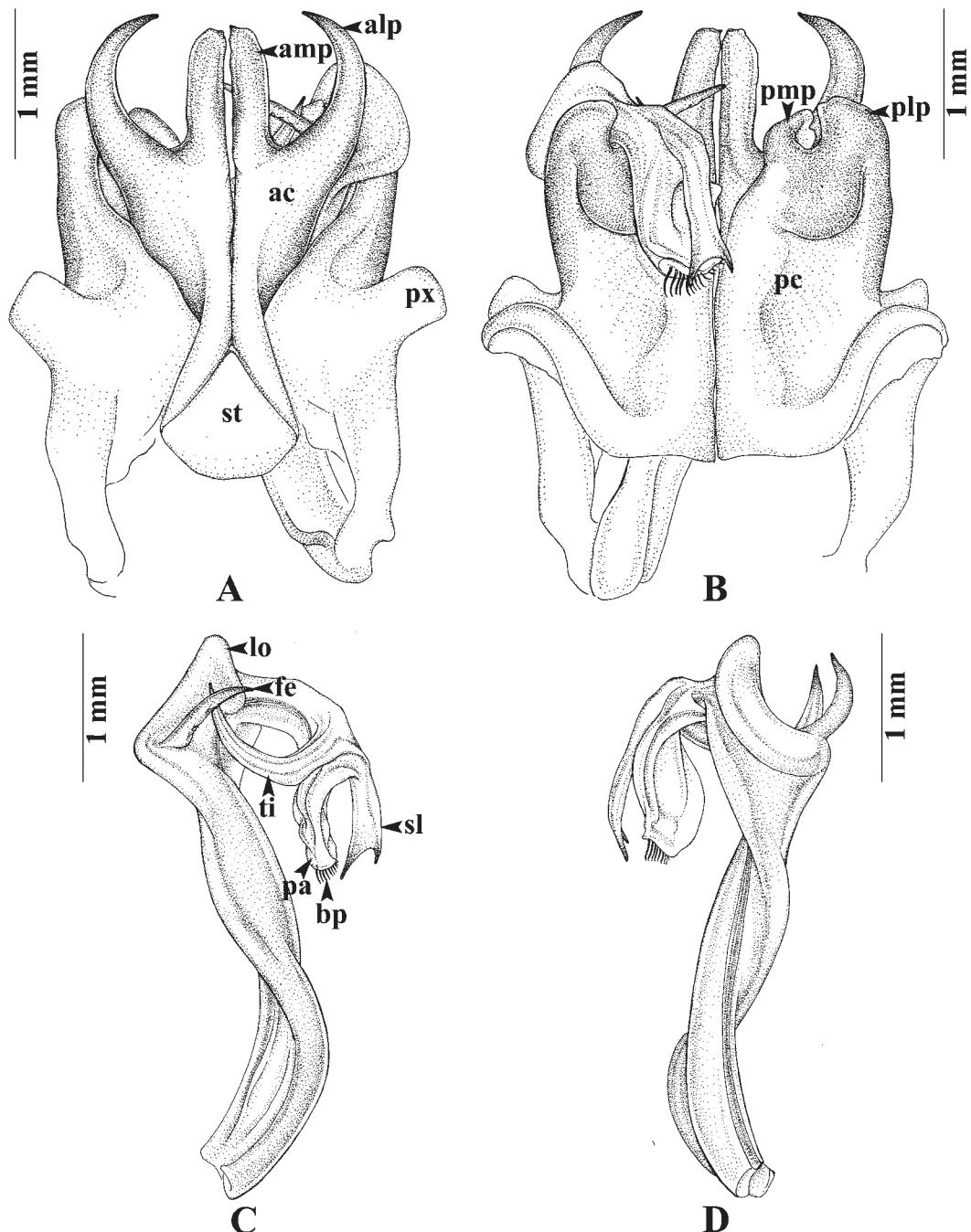
**FIGURE 10.** *Thyropygus bearti*, holotype, gonopods. A: anterior view, left telopodite removed. B: posterior view, left telopodite removed. C: left telopodite, anterior view. D: left telopodite, posterior view.

***Thyropygus bispinispatula* n. sp.**

(Figs. 11A–D, 18C)

**Material:** HOLOTYPE male THAILAND, Chumphon Province, Lang Suan district, Khao Krieab Temple,  $9^{\circ} 49' 4''$  N,  $99^{\circ} 2' 17''$  E. 11 October 2008. P. Prasankok and members of Animal Systematics Research Unit leg., (CUMZ). – Paratypes: 2 females and 3 juveniles, same data as holotype (CUMZ).

**Etymology:** The species epithet is a Latin noun in apposition and refers to the spinose spatulate lobe of the gonopod telopodite.



**FIGURE 11.** *Thryopygus bispinispatula*, holotype, gonopods. A: anterior view, left telopodite removed. B: posterior view, left telopodite removed. C: left telopodite, anterior view. D: left telopodite, posterior view.

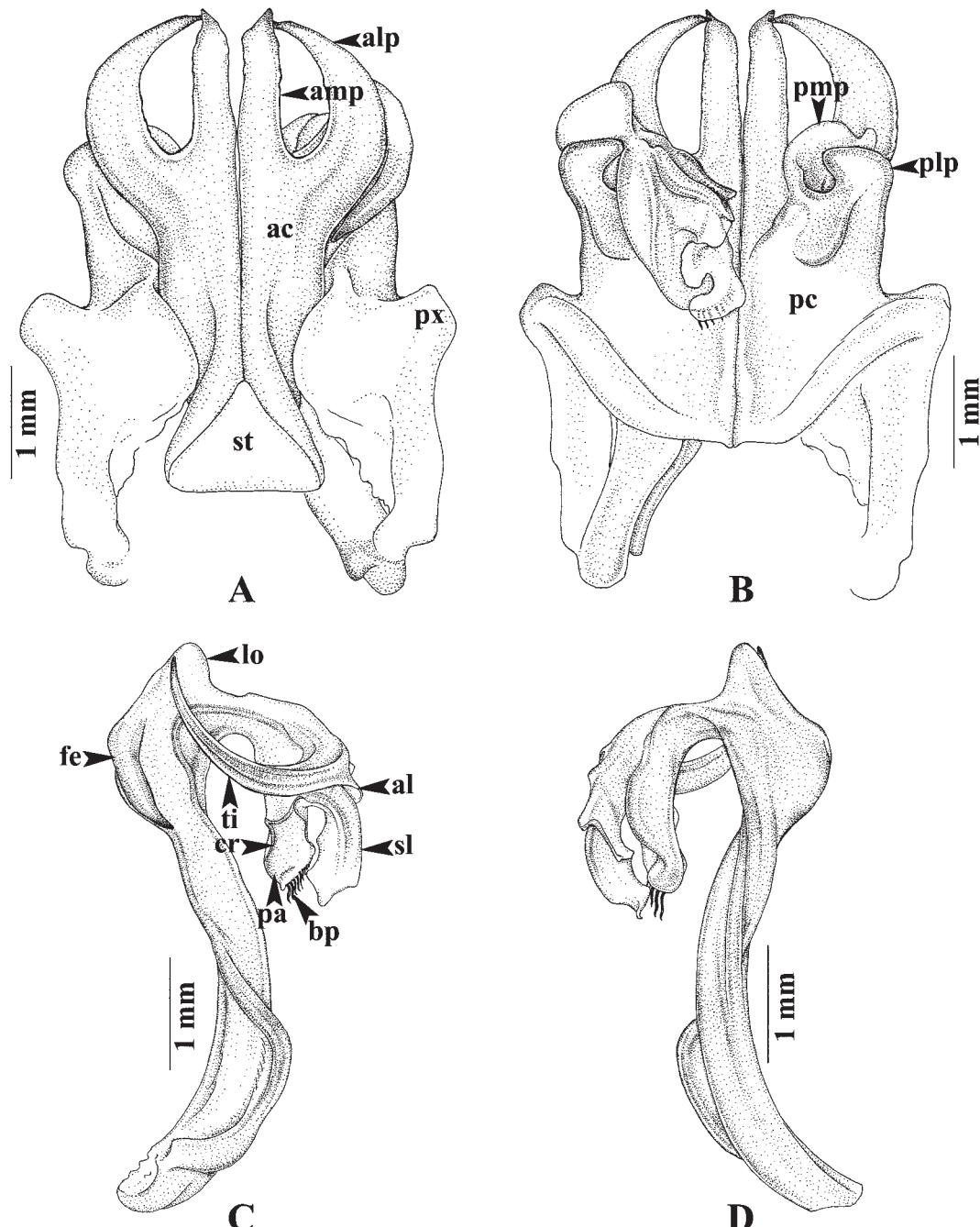
**Diagnosis:** A species of the *opinatus* subgroup. Differing from all other species in the subgroup by having the spatulate lobe (*sl*) at the apical part of telopodite terminating in two sharp brown spines.

**Description:** Adult males with 67 podous rings, no apodous rings. Length ca. 12 cm, width ca. 7.4 mm. Adult females with 64 podous rings, no apodous rings. Length ca. 13–16 cm, width ca. 7.6–9.3 mm. Overall color of living animal (Fig. 18C) yellowish brown. Legs and antennae brownish orange. Paraprocts dark brown.

Gonopods (Figs. 11A–D): Anterior coxal fold (*ac*) (Fig. 11A): lateral process (*alp*) slender, slightly curved mesad; mesal process (*amp*) almost as long as *alp*, straight, flattened, parallel-sided, directed straight distad. Posterior coxal fold (*pc*) (Fig. 11B) basally with moderately high lateral paracoxites (*px*), distally with

two processes: mesal process (*pmp*) slightly shorter than *plp*, and curving behind *plp*; lateral process (*plp*) a rounded lobe, curving caudad. Telopodite (Figs. 11C–D) leaving coxite between *pmp* and *plp*; Femoral spine (*fe*) very long, directed obliquely distad, crenulated along inner curvature, *in situ* resting against posterior surface of *amp*; telopodite distally to *fe* with a vertical, smooth lobe (*lo*) projecting distolaterad; tibial spine (*ti*) very long, curving in horizontal plane close to the middle part of *fe*; spatulate lobe (*sl*) terminating in two sharp brown spines, the outer spine slightly smaller and shorter than the inner one; palette (*pa*) simple, gutter-like, distally with about seven brownish blepharochaetae (*bp*).

**Distribution** (Fig. 20): Known only from the type locality.



**FIGURE 12.** *Thyropygus bispinus*, holotype, gonopods. A: anterior view, left telopodite removed. B: posterior view, left telopodite removed. C: left telopodite, anterior view. D: left telopodite, posterior view.

***Thyropygus bispinus* n. sp.**

(Figs. 12A–D)

**Material:** HOLOTYPE male THAILAND, Uthaithani Province, Tap-Tan district, 15° 29' 11" N, 99° 48' 48" E. July 1996. T. Werner leg., (ZSM). – Paratype: 1 male THAILAND, 2 km East of Mae Lai subdistrict, Muang district, Phrae Province, 80 km East of Lampang Province, 18° 13' 21" N, 100° 12' 30" E. 20 August 1987. T. Werner leg., (ZSM).

**Etymology:** The name refers to the presence of only two spines on the gonopod telopodite – one of the characters that separate this species from the otherwise very similar *T. inflexus*.

**Diagnosis:** A species of the *opinatus* subgroup. Spatulate lobe (*sl*) at the apical part of telopodite expanded, smooth and without a spine. Similar in these respects to *T. inflexus*, *T. bearti*, *T. chelatus*, *T. cristagalli*, *T. brachyacanthus* and *T. loxia*. Differs from the last five of these species by having the mesal process of anterior coxal fold (*amp*) longer than lateral process of anterior coxal fold (*alp*) and tip of *alp* overlapping tip of *amp*. Particularly similar to *T. inflexus*, but differing from it by *amp* being apically sharp, by lateral process of posterior coxal fold (*plp*) being large, rounded, pointing mesad, by the presence of a telopodite lobe (*lo*), by femoral spine (*fe*), being long, by margins of spatulate lobe (*sl*) terminally meeting in a distinct angle and by the absence of a small spine (*ss*) on the gonopod telopodite, opposite the tibial spine.

**Description:** Adult male with 61 podous rings, no apodous rings. Length ca. 10 cm (broken), width ca. 7.0 mm. Color in life unknown; preserved specimen brown.

Gonopods (Figs. 12A–D): Anterior coxal fold (*ac*) (Fig. 12A), lateral process (*alp*) long, slender, regularly curved, sickle-shaped; mesal process (*amp*) slightly longer than lateral process (*alp*), protruding from the middle of the mesal margin of *ac*, apically sharp. Posterior coxal fold (*pc*) (Fig. 12B) basally with moderately high lateral paracoxites (*px*), distally with two processes: mesal process (*pmp*) flattened, curving behind *plp*; lateral process (*plp*) a rounded lobe, projecting further caudad. Telopodite (Figs. 12C–D) leaving coxite between *pmp* and *plp*; femoral spine (*fe*) flattened, very long, *in situ* resting close to middle part of *ac*; telopodite distally to *fe* with a round lobe (*lo*) projecting distolaterally; tibial spine (*ti*) long, slender, recurved and almost reaching tip of *lo*; margins of spatulate lobe (*sl*) terminally meeting in a distinct angle (but not forming a spine), lateral margin of *sl* twisted; a small accessory lobe (*al*) at base of *sl* and a twisted lamella behind *sl*; palette (*pa*) simple, gutter-like, with a longitudinal rounded crest (*cr*) near tip, distally with about nine brownish blepharochaetae (*bp*).

**Distribution** (Fig. 20): Known only from the type locality in central Thailand and one additional locality in northern Thailand, the two sites being separated by approximately 365 km.

***Thyropygus brachyacanthus* n. sp.**

(Figs. 13A–D, 18D)

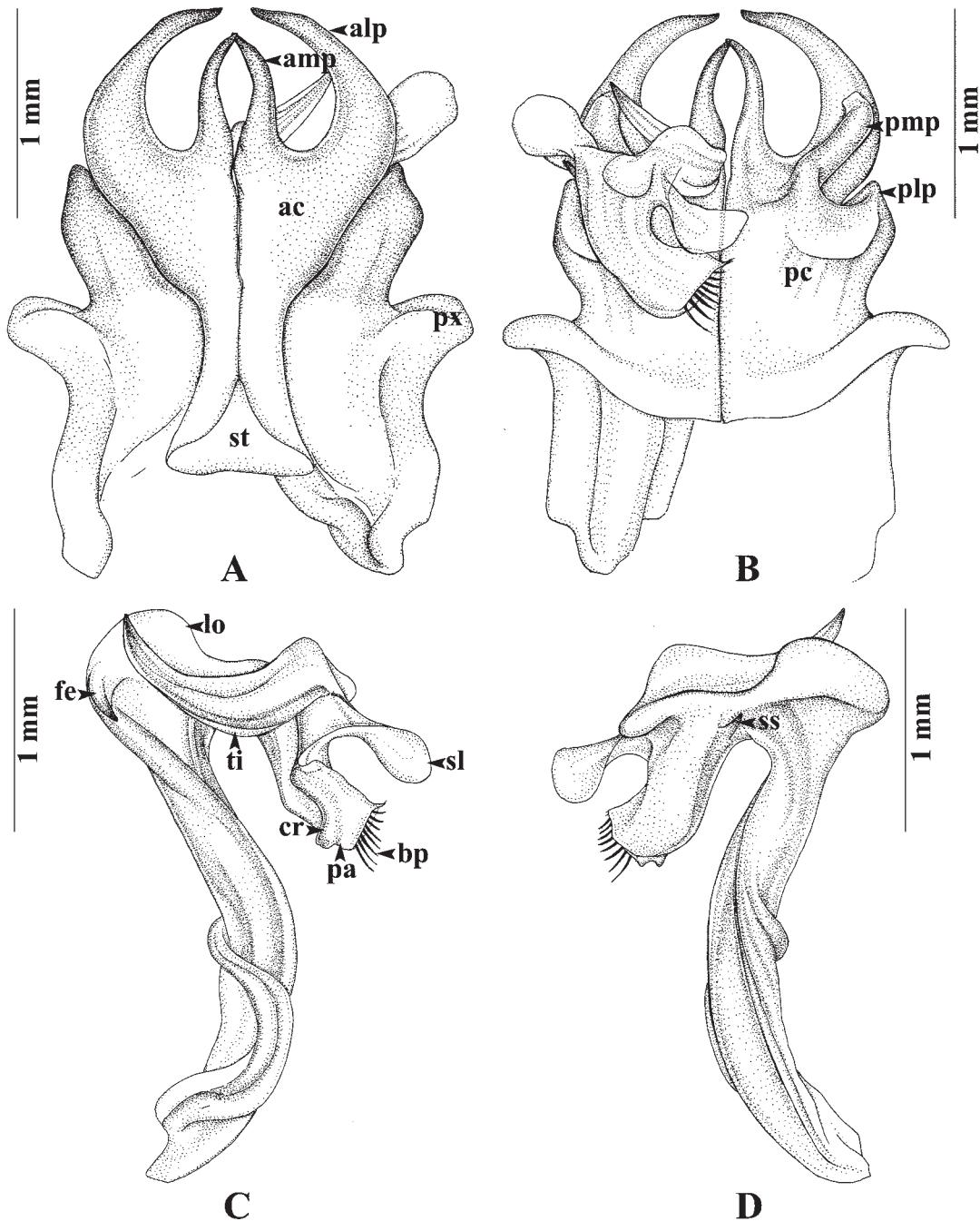
**Material:** HOLOTYPE male THAILAND, Suratthani Province, Khiriratnikhom district, Sathitkhirirom Temple, 9° 01' 49" N, 98° 59' 12" E. 9 October 2008. H. Enghoff, S. Panha, P. Pimvichai and members of Animal Systematics Research Unit leg., (CUMZ). – Paratypes: 5 males, 5 females, same data as holotype (CUMZ), 2 males, 2 females (ZMUC), 1 male, 1 female, THAILAND, Suratthani Province, Ban Takhun district, Water supply Khaowong, 8° 56' 5" N, 98° 55' 30" E. 9 October 2008. H. Enghoff, S. Panha, P. Pimvichai and members of Animal Systematics Research Unit leg., (CUMZ).

**Etymology:** The species epithet is a Greek noun in apposition and refers to the short femoral spine of the gonopod telopodite.

**Diagnosis:** A species of the *opinatus* subgroup. Spatulate lobe (*sl*) at the apical part of telopodite rounded, spoon-like. Similar in this respect to *T. inflexus*, *T. bearti*, *T. chelatus*, *T. cristagalli* and *T. loxia*. Differs from all other species of the *T. opinatus* subgroup by having the lateral process of anterior coxal fold (*alp*) flattened, regularly curved, sickle-shaped, and by having the mesal process (*amp*) almost as long as *alp*, directed distad,

slightly sigmoid, pointed

**Description:** Adult males with 63–67 podous rings, no apodous rings. Length ca. 10–11 cm, width ca. 4.5–5.1 mm. Adult females with 62–65 podous rings, no apodous rings. Length ca. 10–13 cm, width ca. 5.6–6.7 mm. Overall color of living animal (Fig. 18D) grayish black. Metazona dark brown. Legs pink. Epiproct, paraprocts reddish orange.

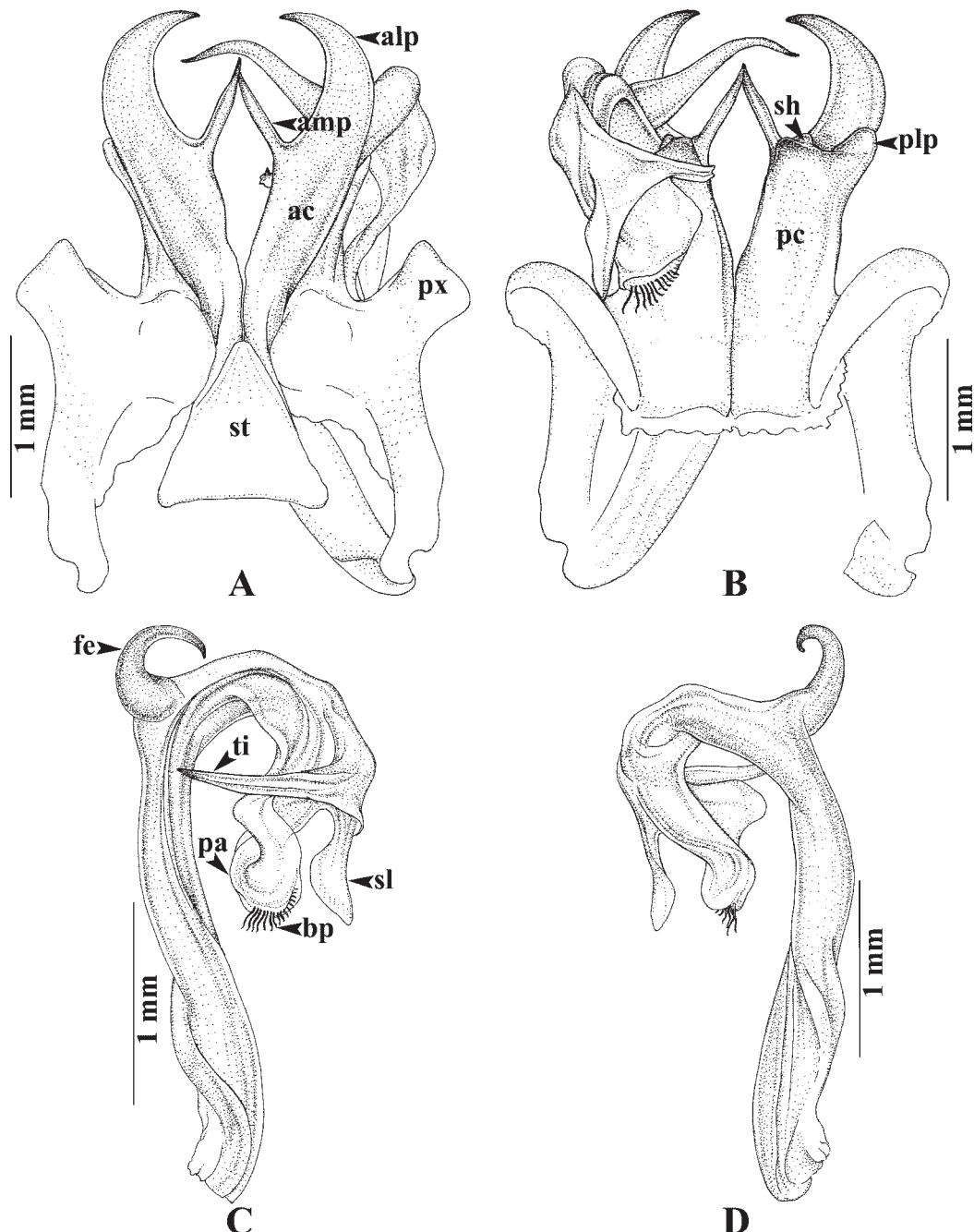


**FIGURE 13.** *Thyropygus brachyacanthus*, holotype, gonopods. A: anterior view, left telopodite removed. B: posterior view, left telopodite removed. C: left telopodite, anterior view. D: left telopodite, posterior view.

Gonopods (Figs. 13A–D): Anterior coxal fold (*ac*) (Fig. 13A): lateral process (*alp*) flattened, long, slender, regularly curved; mesal process (*amp*) almost as long as *alp*, directed distad, slightly sigmoid, pointed. Posterior coxal fold (*pc*) (Fig. 13B) basally with moderately high lateral paracoxites (*px*), distally truncate, forming shelf (*sh*) for accommodation of telopodite; mesal process (*pmp*) directed distolaterad.

Telopodite (Figs. 13C–D) leaving coxite over shelf of posterior coxal fold; Femoral spine (*fe*) short, slightly curved, *in situ* resting behind *alp*; telopodite distally to *fe* with a round lobe (*lo*) projecting distolaterad; tibial spine (*ti*) very long, curving in horizontal plane, *in situ* resting close to tip of *pmp*; an additional protruding lamella at the origin of *ti*; spatulate lobe (*sl*) basally slender, distally broadly expanded; a small slender spine (*ss*) at base of apical part, opposite the origin of the tibial spine; palette (*pa*) simple, gutter-like, with a longitudinal rounded crest (*cr*) near tip, distally with about eight brownish blepharochaetae (*bp*).

**Distribution** (Fig. 20): Known only from the type locality and one further site in Suratthani Province, the two sites being separated by approximately 25 km.



**FIGURE 14.** *Thyropygus chelatus*, paratype, gonopods. A: anterior view, left telopodite removed. B: posterior view, left telopodite removed. C: left telopodite, anterior view. D: left telopodite, posterior view.

***Thyropygus chelatus* n. sp.**

(Figs. 4, 14A–D, 19A)

**Material:** HOLOTYPE male THAILAND, Nakhonsrithammarat Province, Khanom district, Koh Rab, 9° 18' 30" N, 99° 57' 30" E. 26 August 2007. H. Enghoff and S. Panha leg., (CUMZ). – Paratypes: 10 males, 40 females, same data as holotype (CUMZ), 2 males, 2 females, same data as holotype (ZMUC), 3 males, 2 females, THAILAND, Nakhonsrithammarat Province, Khanom district, Koh Wangnok, 9° 14' 41" N, 99° 54' 48" E. 26 August 2007. H. Enghoff and S. Panha leg., (CUMZ).

**Etymology:** The name refers to the chela-like gonopodal anterior coxal fold.

**Diagnosis:** A species of the *opinatus* subgroup. Spatulate lobe (*sl*) at the apical part of telopodite rounded, spoon-like. Similar in this respect to *T. inflexus*, *T. bearti*, *T. cristagalli*, *T. brachyacanthus* and *T. loxia*. Differs from these species by the mesal process of anterior coxal fold (*amp*) being directed obliquely meso-distad from the mesal margin of anterior coxal fold (*ac*).

**Description:** Adult males with 56–58 podous rings, no apodous rings. Length ca. 9–12 cm, width ca. 6.8–7.2 mm. Adult females with 54–60 podous rings, no apodous rings. Length ca. 10–12 cm, width ca. 7.2–8.0 mm. Overall color of living animal (Fig. 19A) medium brown. Prozona, legs and antennae brown, metazona dark brown, head reddish brown, tip of epiproct, margins of paraprocts, and hypoproct yellow.

Gonopods (Figs. 14A–D): Sternum (*st*) somewhat larger than in the other subgroup members. Anterior coxal fold (*ac*) (Fig. 14A): lateral process (*alp*) stout, regularly sickle-shaped; mesal process (*amp*) much shorter than lateral process, directed obliquely disto-mesad, slender, straight, and pointed. Posterior coxal fold (*pc*) (Fig. 14B) basally with moderately high lateral paracoxites (*px*), distally truncate, forming shelf (*sh*) for accommodation of telopodite; laterally with an erect, digitiform process (*plp*). Telopodite (Figs. 14C–D) leaving coxite over shelf of posterior coxal fold; femoral spine (*fe*) long, slender, excavated along its outer curvature, curving almost exclusively in horizontal plane, its outer curvature *in situ* resting against the processes *alp* and *amp*; tibial spine of same size and shape as femoral spine, but curving in the opposite direction in the horizontal plane, its tip *in situ* resting against mesal corner of shelf (*sh*); apical part: spatulate lobe (*sl*) basally slender, distally expanded, rounded, spoon-like; palette (*pa*) simple, gutter-like, distally with about twelve brownish blepharochaetae (*bp*).

**Distribution** (Fig. 20): Known only from Koh Rab and Koh Wangnok, two small islands in the Gulf of Thailand, where it was very abundant on the day of collecting.

***Thyropygus cristagalli* n. sp.**

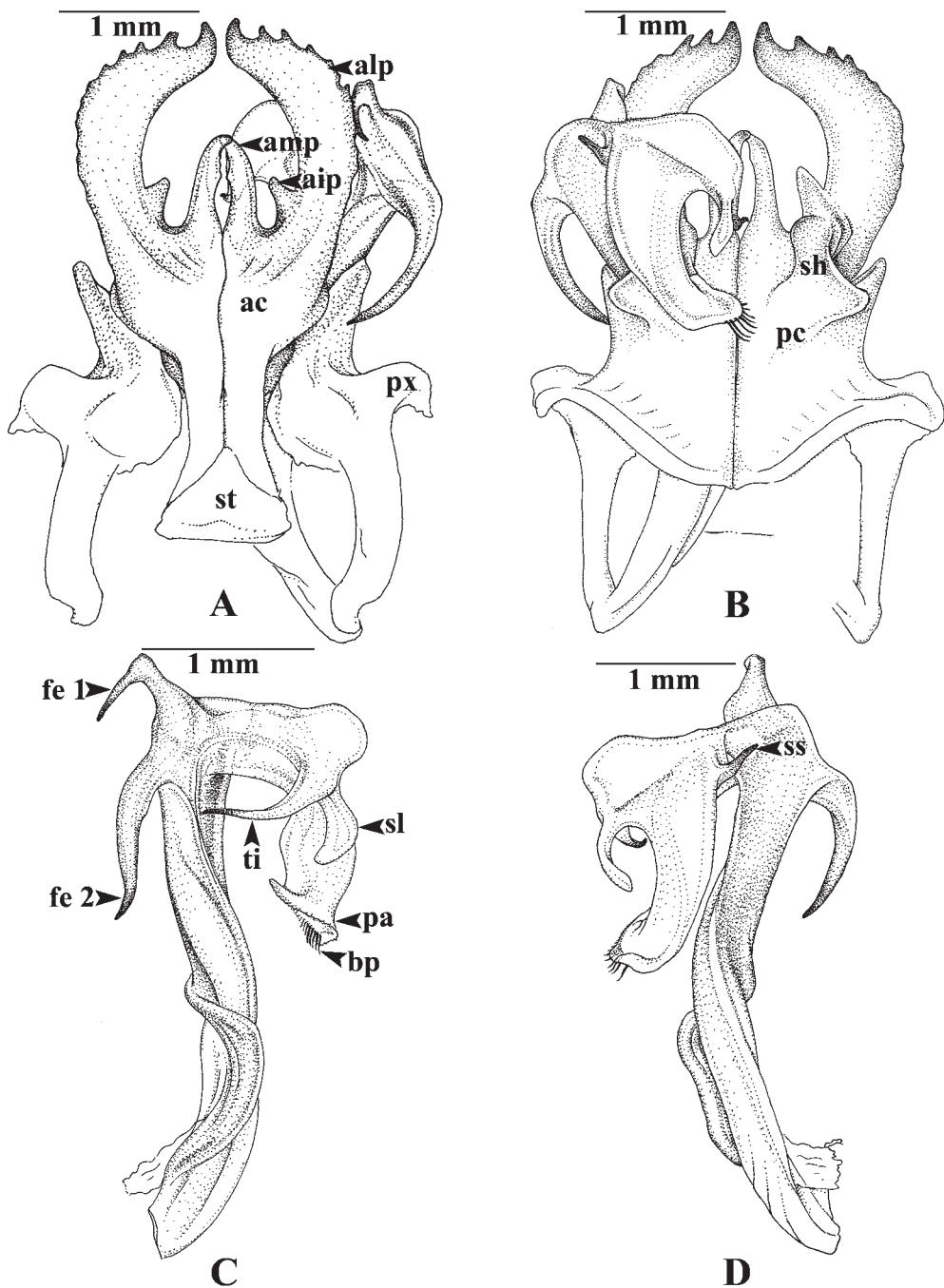
(Figs. 15A–D, 19B)

**Material:** HOLOTYPE male THAILAND, Phang Nga Province, Koh Yao district, Koh Yao Noi, 8° 06' 45" N, 98° 36' 6" E. 2 May 2007. P. Pimvichai and P. Prasankok leg., (CUMZ). – Paratypes: 7 males, 8 females, same data as holotype (CUMZ), 2 males, 2 females, same data as holotype (ZMUC).

**Etymology:** The species epithet is a Latin noun in apposition, meaning cockscomb, and refers to the shape of the lateral process of the anterior gonopod coxal fold (*alp*).

**Diagnosis:** A species of the *opinatus* subgroup. Spatulate lobe (*sl*) at the apical part of telopodite rounded, spoon-like. Similar in this respect to *T. inflexus*, *T. bearti*, *T. chelatus*, *T. brachyacanthus* and *T. loxia*. Differs from all other species of the *T. opinatus* subgroup by having the femoral spine (*fe*) doubled, and by having the laterodistal margin of the lateral process of the anterior coxal fold (*alp*) coarsely serrate, cockscomb-like.

**Description:** Adult males with 61 podous rings, no apodous rings. Length ca. 11–14 cm, width ca. 7.6–7.9 mm. Adult females with 56–61 podous rings, no apodous rings. Length ca. 8–12 cm, width ca. 6.6–7.7 mm. Overall color of living animal (Fig. 19B) brown with a longitudinal reddish band mid-dorsally on the body. Legs, head, and antennae darker brown.

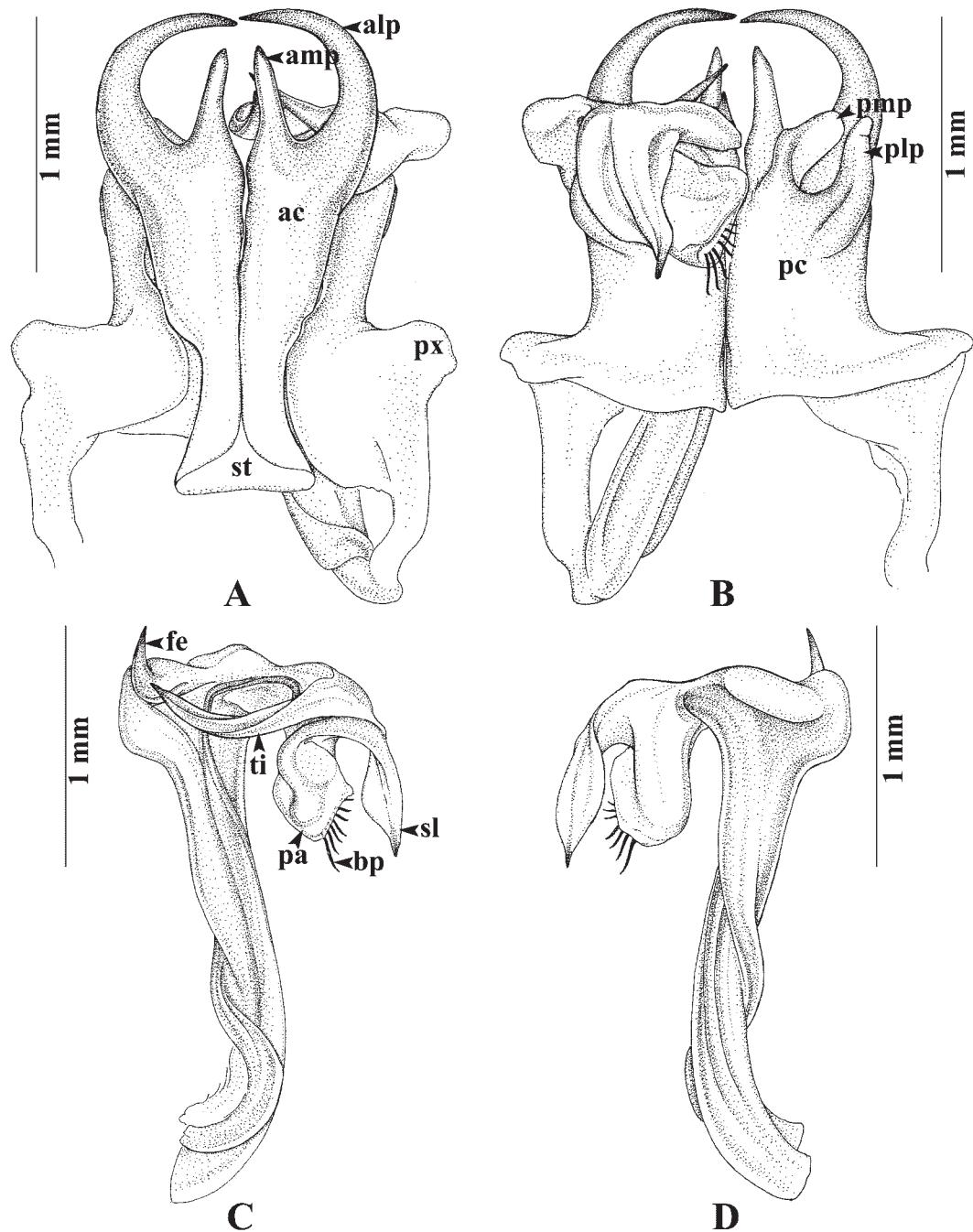


**FIGURE 15.** *Thyropygus cristagalli*, paratype, gonopods. A: anterior view, left telopodite removed. B: posterior view, left telopodite removed. C: left telopodite, anterior view. D: left telopodite, posterior view.

Gonopods (Figs. 15A–D): Anterior coxal fold (*ac*) (Fig. 15A): lateral process (*alp*) flattened, slightly curved, its laterodistal margin coarsely dentate, terminating in a short, pointed spine; an additional spine-like process (*aip*) between *alp* and *amp*, *aip* in lateral view broadly triangular; mesal process (*amp*) much shorter than *alp*, directed distad, curving very slightly mesad, pointed. Posterior coxal fold (*pc*) (Fig. 15B) basally with moderately high lateral paracoxites (*px*), distally truncate, forming shelf (*sh*) for accommodation of telopodite; Telopodite (Figs. 15C–D) leaving coxite over shelf of posterior coxal fold; femoral spine (*fe*) duplicated, one spine (*fe* 1) much smaller than the other, basally broad and erect, ending in a slender barb, the second (*fe* 2) longer and thicker than *fe* 1, situated under *fe* 1, almost straight, slightly sigmoid, its tip *in situ* resting close to the middle part of *ac*; tibial spine (*ti*) long, slender and recurved, curving in horizontal plane,

its tip *in situ* resting at the base of *amp*; apical part: spatulate lobe (*sl*) basally slender, distally expanded, rounded, slightly twisted; a small slender spine (*ss*) at base of apical part, opposite the origin of the tibial spine; palette (*pa*) simple, in the middle with a small lateral lamella, distally with about twelve brownish blepharochaetae (*bp*).

**Distribution** (Fig. 20): Known only from the type locality.



**FIGURE 16.** *Thyropygus erectus*, holotype, gonopods. A: anterior view, left telopodite removed. B: posterior view, left telopodite removed. C: left telopodite, anterior view. D: left telopodite, posterior view.

***Thyropygus erectus* n. sp.**

(Figs. 16A–D, 19C)

**Material:** HOLOTYPE male THAILAND, Satun Province, La-Ngu district, Koh Tarutao, 6° 49' 36" N, 99° 38' 30" E. 6 April 2008. P. Pimvichai, P. Prasankok, P. Tongkerd, R. Chanabun and Suwit Lhaokhum leg., (CUMZ). – Paratypes: 10 females, same data as holotype (CUMZ).

**Etymology:** The species epithet is a Latin adjective and refers to the erect femoral spine of the gonopod telopodite.

**Diagnosis:** A species of the *opinatus* subgroup. Spatulate lobe (*sl*) at the apical part of telopodite terminating in a sharp brown spine. Similar in this respect to *T. opinatus*, *T. floweri* and *T. implicatus*. Differs from these species by having the femoral spine (*fe*) directed distad and by having the mesal process of posterior coxal fold (*pmp*) flattened, curved distolaterad.

**Description:** Adult male with 56 podous rings, no apodous rings. Length ca. 7 cm, width ca. 4.3 mm. Adult females with 53–58 podous rings, no apodous rings. Length ca. 8–10 cm, width ca. 4.6–5.6 mm. Overall color of living animal (Fig. 19C) brown with a longitudinal orange band mid-dorsally on the body. Legs and antennae pale pink. Epiproct and margins of paraprocts yellow.

Gonopods (Figs. 16A–D): Anterior coxal fold (*ac*) (Fig. 16A): lateral process (*alp*) long, slender, regularly curved, tip close to tip of opposite *alp*, the two together forming a circle; mesal process (*amp*) almost as long as *alp*, straight, directed distad. Posterior coxal fold (*pc*) (Fig. 16B) with lateral paracoxites (*px*) quite low, lateral process (*plp*) digitiform; mesal process (*pmp*) flattened, curved distolaterad. Telopodite (Figs. 16C–D) leaving coxite between *pmp* and *plp*; femoral spine (*fe*) situated on the broad rounded lobe, directed distad, *in situ* resting close to *amp*; tibial spine (*ti*) very long, slender, curving in horizontal plane, its tip close to base of *fe*, *in situ* resting between *amp* and *alp*; apical part: spatulate lobe (*sl*) with a sharp dark brown spine at tip; palette (*pa*) simple, distally with about six brownish blepharochaetae (*bp*).

**Distribution** (Fig. 20): Known only from the type locality.

***Thyropygus loxia* n. sp.**

(Figs. 17A–D, 19D)

**Material:** HOLOTYPE male THAILAND, Suratthani Province, Thachana district, Tam-Yai Temple, 9° 33' 31" N, 99° 10' 26" E. 11 October 2008. H. Enghoff, S. Panha, P. Pimvichai and members of Animal Systematics Research Unit leg., (CUMZ). – Paratypes: 1 female and 2 sub-adult males, same data as holotype (CUMZ).

**Etymology:** The name refers to the overlapping lateral processes of the gonopod anterior coxal folds, reminiscent of the bill in the bird genus *Loxia* (crossbills).

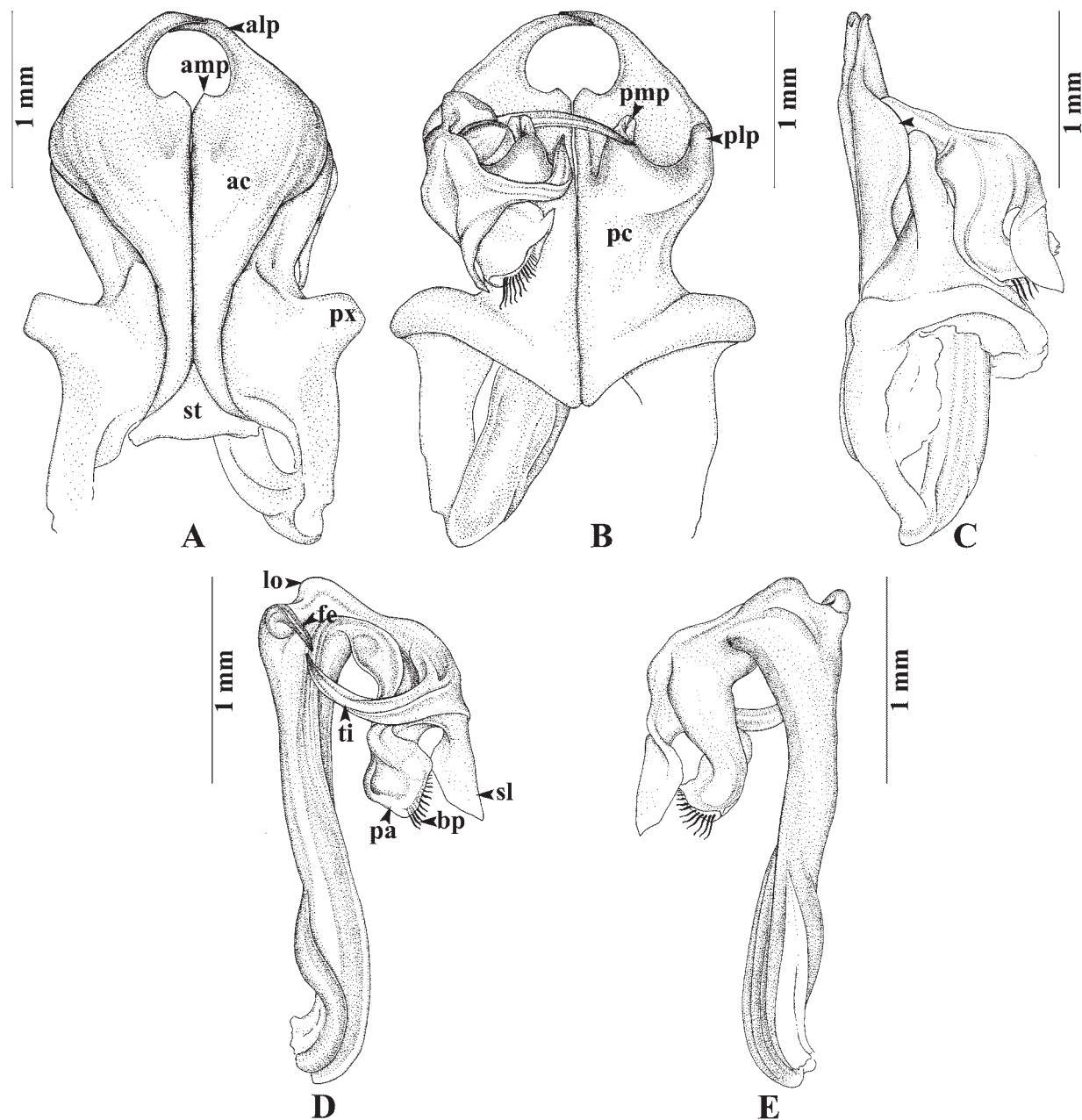
**Diagnosis:** A species of the *opinatus* subgroup. Spatulate lobe (*sl*) at the apical part of telopodite rounded, spoon-like. Similar in this respect to *T. inflexus*, *T. bearti*, *T. chelatus*, *T. cristagalli* and *T. brachyacanthus*. Differs from all other species of the *T. opinatus* subgroup by having a longitudinal lateral crest (Fig 17C, arrow) on the anterior coxal fold (*ac*); by having the tip of the lateral process of anterior coxal fold (*alp*) crossing over with opposite tip, and by having the median process of posterior coxal fold (*amp*) very small.

**Description:** Adult male with 69 podous rings, no apodous rings. Length ca. 10 cm, width ca. 5.5 mm. Adult female with 58 podous rings, no apodous rings. Length ca. 9 cm, width ca. 6.3 mm. Overall color of living animal (Fig. 19D) brown. Antennae and legs brownish orange.

Gonopods (Figs. 17A–E): Anterior coxal fold (*ac*) (Figs. 17A, C) with a lateral longitudinal crest (Fig. 17C, arrow); lateral process (*alp*) slender, regularly curved, tip crossing over with tip of opposite side, the two together forming a circle; mesal process (*amp*) very small, hump-like. Posterior coxal fold (*pc*) (Fig. 17B) basally with moderately high lateral paracoxites (*px*), distally with two processes: mesal process (*pmp*) curving caudad; lateral process (*plp*) digitiform, directed distad. Telopodite (Figs. 16D–E) leaving coxite

between *pmp* and *plp*; femoral spine (*fe*) very long, curved, *in situ* resting curving close to *pmp*; telopodite distally to *fe* with a small round lobe (*lo*) projecting distolaterad; tibial spine (*ti*) very long, curving in horizontal plane under *fe*, *in situ* resting close to mesal part of *fe*; spatulate lobe (*sl*) basally slender, distally broadly expanded, rounded, spoon-like; palette (*pa*) simple, gutter-like, distally with about eight brownish blepharochaetae (*bp*).

**Distribution** (Fig. 20): Known only from the type locality.



**FIGURE 17.** *Thyropygus loxia*, holotype, gonopods. A: anterior view, left telopodite removed. B: posterior view, left telopodite removed. C: lateral view. D: left telopodite, anterior view. E: left telopodite, posterior view.



**A**



**B**



**C**



**D**

**FIGURE 18.** A: *Thyropygus opinatus*, living male. B: *Thyropygus bearti*, living male. C: *Thyropygus bispinispatula*, living male. D: *Thyropygus brachyacanthus*, living male.



**FIGURE 19.** A: *Thyropygus chelatus*, living male. B: *Thyropygus cristagalli*, living male. C: *Thyropygus erectus*, living male. D: *Thyropygus loxia*, living female.

## Discussion

This paper is the first in a planned series of papers on the *Thyropygus allevatus* group. We have followed the concept of the *allevatus* group presented by Hoffman (1975), updated with new species and taxonomic changes since 1975. We have also followed Hoffman (1975) with regard to the identity of the genus *Thyropygus*, and we have formalized the synonymization of *Cornugonus* under *Thyropygus*, tentatively suggested by Hoffman (1975) and Demange (1989).

We have initiated the division of the *T. allevatus* group into subgroups and in this paper treat one of these, the *T. opinatus* subgroup which corresponds, *grosso modo*, to the genus *Cornugonus sensu* Demange (1961).

We are aware that future studies may result in re-definitions at all levels: the genus *Thyropygus*, the *T.*

*allevatus* group, and the *T. opinatus* subgroup. At present, these groupings are defined exclusively on the basis of a few morphological characters, the phylogenetic significance of which remains unassessed. The discussion of individual characters, below, makes the shaky foundation of our grouping quite evident. We hope that future phylogenetic studies involving molecular as well as morphological characters will shed light over the relationships within this group of large to gigantic millipedes.

The species within the *T. opinatus* subgroup share a general similarity of gonopodal characters. Notably, they all have two distinct processes on the anterior coxal fold, and they all have a spatulate lobe close to the tibial spine.

On the other hand, we also found important variations in several gonopodal characters within this subgroup. Thus:

- the femoral spine (*fe*) is simple in all species except *T. cristagalli* which has *fe* duplicated and in this respect resembles the species of the *T. bifurcus* group.

- the spatulate lobe (*sl*) has a distal sharp, dark brown spine in *T. opinatus*, *T. floweri*, *T. implicatus*, and *T. erectus*; in *T. bispinispatula* there are two such spines, but in *T. inflexus*, *T. bearti*, *T. chelatus*, *T. cristagalli*, *T. brachyacanthus*, and *T. loxia* it is distally expanded, smooth and rounded, and has no spine. In *T. bispinus*, the margins of the spatulate lobe meet terminally in a distinct angle but do not form a spine.

- the mesal process (*amp*) of the anterior coxal fold is directed distad in all species except *T. chelatus* in which it is protruding obliquely disto-mesad. In *T. loxia* this process is very small, not unlike what one sees in *T. peninsularis* Hoffman, 1982.

- the telopodite lobe (*lo*) is present in *T. opinatus*, *T. floweri*, *T. implicatus*, *T. bispinus*, *T. bispinispatula*, *T. brachyacanthus*, and *T. loxia* but absent in *T. inflexus*, *T. chelatus*, *T. bearti*, *T. cristagalli*, and *T. erectus*.

- a longitudinal rounded crest (*cr*) near the tip of the apical palette (*pa*) is present in *T. opinatus*, *T. bearti*, *T. bispinus*, and *T. brachyacanthus* but absent in *T. floweri*, *T. implicatus*, *T. inflexus*, *T. chelatus*, *T. cristagalli*, *T. bispinispatula*, *T. loxia*, and *T. erectus*.

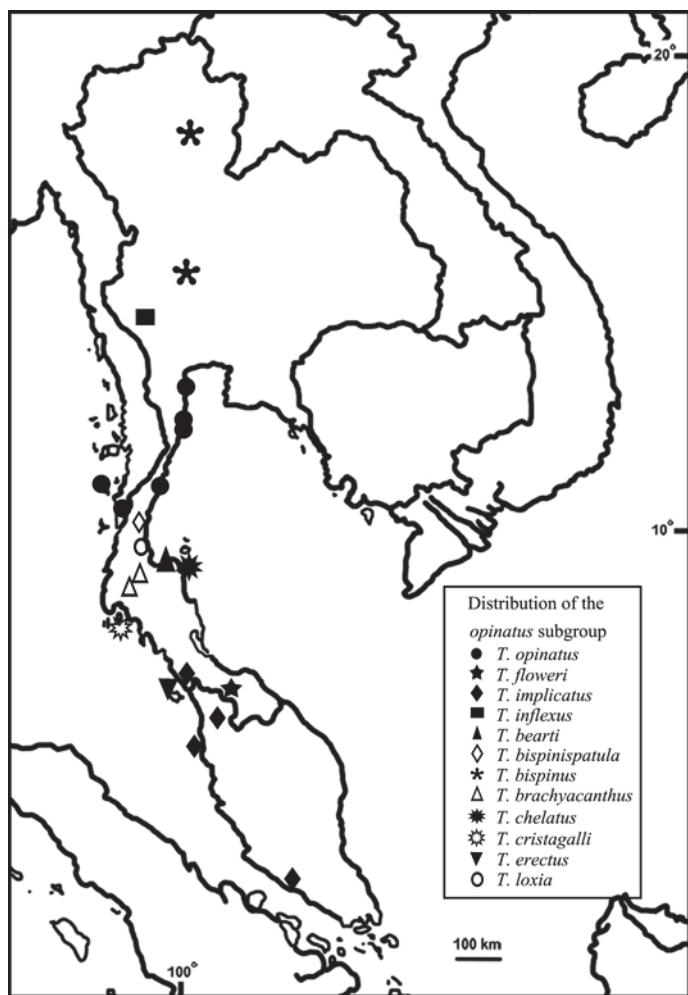
*T. inflexus* and *T. bispinus* are particularly similar in the general shape of the anterior coxal fold but nevertheless differ in a number of characters as described in each species description. Thus, the mesal process (*amp*) of the anterior coxal fold in *T. inflexus* is apically irregularly tuberculate but in *T. bispinus* it is apically sharp; the femoral spine (*fe*) is short in *T. inflexus*, but very long in *T. bispinus*; a small slender spine (*ss*) at the base of the apical part of the telopodite, opposite the origin of the tibial spine, is present in *T. inflexus*, but absent in *T. bispinus*; the lateral process of the anterior coxal fold (*alp*) apically has a crest extending caudad and ending in a small spine, in *T. inflexus*, whereas such a crest is absent in *T. bispinus*.

We suggest that all these characters are useful for recognition of taxa at the species level. Under an alternative point of view, the species recognized by us ('our species') might be regarded as subspecies of a single, widespread species. This would be consistent with the lack of sympatry between any of our species. On the other hand, each of our species differs from all the others by more than one character, the gonopod morphology of each is quite constant, and none of them looks like an intermediate between any set of the others. We therefore have adopted a splitting approach.

The spatulate lobe (*sl*) on the gonopod telopodite is the most diagnostic character of the *T. opinatus* subgroup. Some species outside this subgroup have a superficially similar lateral lamella on the apical part of the telopodite, viz., *T. cuisinieri* Carl, 1917 and *T. carli* Attems, 1938, but this lamella is very slender and sharp. Moreover, these species are characterized by the prominent development of a projecting lobe on the lateral surface of the anterior coxal fold, and we suggest classifying them in a different subgroup.

*T. peninsularis* Hoffman, 1982, has a small spatulate lobe on the apical part of the telopodite, and even a very short additional mesal projection of the gonopod anterior coxal lobe (like *T. loxia*). However, this species does not belong to the *T. allevatus* group because it does not share the group-characteristic shape of the tibial spine.

According to the material we have studied and the available literature, the *T. opinatus* subgroup is distributed from the North to the South of Thailand and in some adjacent areas of Myanmar and Malaysia. The majority of records, however, are from the southern part of Thailand and the Malay Peninsula (Fig. 20).



**FIGURE 20.** Known distribution of the species of the *T. opinatus* subgroup.

#### Acknowledgements

We express our sincere gratitude to the Plant Genetic Conservation Project initiated by her Royal Highness Princess Maha Chakri Sirindhorn, and the Navy Special Warfare Unit of the Royal Thai Navy for their kind assistance and encouragement, which enabled us to pursue the necessary fieldwork at Koh Yao Noi, Phang Nga province and Koh Tarutao, Satun province. We also thank members of Animal Systematics Research Unit, Chulalongkorn University for assistance in collecting material. This research was funded by The Thailand Research Fund, The Royal Golden Jubilee Ph.D. Program (PHD/0015/2549). Additional funding was provided to Somsak Panha by the CHE-RG under the Limestone Biodiversity Project and by the BRT Program (TRF/BIOTECH-Thailand Biodiversity Research and Training Program) under the BRT-Millipede-Earthworm Project. We thank Prof. Dr. Richard L. Hoffman for his useful comments. We further extend our thanks to the curators who provided specimens for our study: Jean-Jacques Geoffroy (MNHN), Jörg Spelda and Stefan Friedrich (ZSM), Urs Wüest (NHMB), to Peter Decker for finding specimens in SMF, to Louis Deharveng (MNHN) for information about the type locality of *T. inflexus*, to Jan Pedersen and Tamás Szüts (ZMUC) for help with photography and scanning electron microscopy, and to Thita Krutchuen for excellent drawings.

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